# DIVING PHYSIOLOGY OF THE RINGED SEAL: ADAPTATIONS, CAPABILITY AND IMPLICATIONS

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# DIVING PHYSIOLOGY OF THE RINGED SEAL: ADAPTATIONS, CAPABILITY AND IMPLICATIONS

A

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ABSTRACT

Adaptations that influence duration of diving in the ringed seal, *Phoca (Pusa) hispida* were examined. Mean blood volume was 234 ml/kg lean body mass (LBM) and oxygen capacity was 30.7 ml $O_2$/100 ml of whole blood, yielding a total blood oxygen capacity of 70 ml $O_2$/kg LBM. Abrupt and prolonged bradycardia occurred upon submersion. Experimental dives indicated submersion durations of up to 18 minutes before the onset of physiological dysfunction. The percentage of LBM represented by the brain is least in the relatively large Weddell seal (0.2%), greater in the harbor seal (0.7%) (the compared species) and greatest in the ringed seal (1.4%); this sets the requirement for minimum obligatory oxygen consumption. The differences observed in diving durations between the three species is considered to be mainly the consequence of brain/body size relationship.

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# INTRODUCTION

## Present and Historical Developments

Adequate oxygenation of tissues is necessary to sustain physiological functions. Tissues with high rates of metabolism and little capacity for anaerobic conversion of energy are particularly susceptible to dysfunction upon reduced oxygen supply. The vertebrate brain is highly dependent on oxidative metabolism to provide energy at a rate sufficient to sustain its active state. Air breathing has assured adequate oxygen intake to meet these demands. However, mammals are frequently exposed to episodes of reduced oxygen supply. Disorders such as suffocation and near drowning are occurrences reducing the ability to oxygenate the blood. Arterial blockage in coronary occlusion and strokes, as well as reduced blood flow during shock and hemorrhage, may lower or terminate the flow of oxygenated blood to localized tissues; thence, physiological dysfunction and cellular deterioration may commence.

Various animals experience common and quite natural (i.e., non-pathological) episodes of reduced oxygenation of the blood and other tissues. This is manifest in birth asphyxia, high altitude breathing and hibernation. Diving mammals, when submersed in water, cannot oxygenate their blood. Under these conditions, physiological and morphological adaptations increase the total oxygen supply, reduce blood flow to tissues capable of anaerobic maintenance, and maintain blood flow to vital tissues and organs requiring oxygen.

Diving mammals are subjects for investigating these adaptations and have been discussed in review articles (Andersen, 1966; Elsner, 1969). In these subjects not only do we find the highly evolved mammalian brain, which is metabolically dependent on oxygen, but we also have subjects that restrict themselves from continual respiration by submergence. For example, the beaver can dive for 15 min (Irving and Orr, 1935). Many marine mammals can submerge for long periods of time. Some seals are capable of submergence for more than 15 min and in some species dives of 30 to 60 min have been observed.

Adaptations to accommodate seals in water are morphological features to assist their swimming, such as flippers and elongated, fusiform body. Thick pelage and/or subcutaneous fat provide insulation for thermoregulation. What is not so obvious however is how the animals avoid asphyxiation when submerged for extended intervals. Many terrestrial animals, man included, can endure submergence for only 2 to 4 min before stress of asphyxiation. During this period, the animal begins to suffocate due to termination of gas exchange, and experiences hypoxia (low oxygen) and hypercapnia (high $CO_2$). Eventual anoxia (complete lack of oxygen) results in death. How then have divers evolved to protect themselves against asphyxiation?

Irving (1939) speculated that, although diving animals have increased oxygen storage capacity, it is inadequate for aerobic metabolism of the entire body during sustained diving. If however, selective distribution of the blood oxygen is realized, then the oxygen stores available may well supply the brain and heart for extended intervals

while removing from continued perfusion those tissues capable of prolonged anaerobic metabolism.

Defenses against asphyxiation are qualitatively common in many animal species. Large blood volumes, elevated hemoglobin and myoglobin concentrations, high oxygen capacity and high packed cell volume are characteristic of diving birds and mammals capable of defending against asphyxia during submersion by providing increased oxygen stores for consumption while gas exchange is interrupted. These stores are several fold greater than the oxygen stores found in man. Yet, the duration of submersion which many of these animals can experience without stress, for instance the phocid seals, may be five to ten times greater than that extrapolated from the oxygen stores alone.

Early investigations (Irving, 1938; Irving, 1939; Scholander, 1940; Grinnell *et al.*, 1941; Irving *et al.*, 1942; Scholander *et al.*, 1942) demonstrated cardiovascular responses to submersion and other induced states of asphyxia such as tracheal clamping. The responses observed included decreased heart rate, selective ischemia of peripheral tissues and organs and maintenance of central arterial blood pressure. They showed that the interaction of these functions conserves the oxygen stores by reducing the availability of oxygen to tissues capable of anaerobic metabolism while, at the same time, continuing to supply oxygen to the organs most sensitive to hypoxia. Not only is oxygen conserved for vital function, but it is also delivered via a circulatory system at maintained blood pressure, although a profound decrease in heart rate is experienced.

In some species of marine mammals these adaptations are most dramatic. Some exemplary blood volumes, oxygen capacities, hemoglobin concentrations and packed cell volumes (PCV) are presented in Tables 1 through 3. The high degree to which these variables have evolved in seals is evident. Comparisons of diving durations further exemplify the profound nature of these adaptations in seals (Table 4).

The understanding of the physiological adaptations of animals to defend against submersion asphyxia has advanced considerably during the past fifty years. Investigators have demonstrated the importance of selective ischemia and elevated oxygen stores as defenses against asphyxia (Irving, 1939; Scholander, 1940; Elsner *et al.*, 1966; Elsner *et al.*, 1970c). More recent studies have investigated organ function capability during asphyxia, particularly of the kidney (Murdaugh *et al.*, 1961a; Halasz *et al.*, 1974), the brain (Elsner *et al.*, 1970b; Kerem and Elsner, 1973a; Kerem and Elsner, 1973b), and the heart (Blix *et al.*, 1975b). Relative to organ function, adaptations are being investigated to examine the processes at molecular levels which facilitate maintenance of homeostasis during asphyxic episodes (Reichelt, 1968; Robin and Murdaugh, 1967; Shoubridge *et al.*, 1976; Kerem and Elsner, 1973a,b).

Mechanisms of cardiovascular control have been investigated (Angell-James and Daly, 1972), as well as the reflex mechanisms and neural pathways responsible for elicitation of the cardiovascular responses (Anderson, 1963a).

These research achievements have been powerful in developing the concepts of mechanisms defending against asphyxia. The results and

Table 1. Comparative blood volume data for some

| Species | No. of specimens | *BV/TBM (ml/kg) |
|---|---|---|
| Man (lean) | | |
| Dog | 8 | 92.0 |
| Harbor seal *Phoca vitulina* (4 determinations total) | 2 | 150 |
| Elephant seal *Mirounga angustirostris* | 7 | 216 |
| Weddell seal *Leptonychotes weddelli* | 2 | 148 |

*BV/TBM = blood volume/total body mass; BV/LBM = % BV/LBM = % blood volume/lean body mass.

terrestrial and marine mammals.

| *BV/LBM (ml/kg) | *BV/LBM % | Methods | Reference |
|---|---|---|---|
| 79 | 7.9 | , | Guyton (1971) |
| | | $^{32}p$ T-1824 | Reeve *et al.* (1953) |
| 213 | 21.3 | $^{131}I$ $H_3O$ | Ferren (this paper) |
| | | | Simpson, *et al.* (1970) |
| 197 | 19.7 | | Lenfant *et al.* (1969) |

blood volume/lean body mass;

Table 2. Comparative oxygen capacity data for some terrestrial and marine mammals.

| Species | No. of specimens | PCV (%) | HB (gm%) | $O_2$ capacity ml $O_2$/100 ml (blood) | *$O_2$ combining capacity | †Derived $O_2$ capacity | Reference |
|---|---|---|---|---|---|---|---|
| Man | | | | 20.7 | | | Bock *et al.* (1924) |
| Dog | | | | 21.8 | | | Dill *et al.* (1932) |
| Harbor seal | 8 | | 16.5 | 29.30 | 1.78 | ‡22.8 | Irving *et al.* (1935) |
| *Phoca vitulina* | 5 | | 20.0 | 26.43 | 1.32 | ‡27.6 | Lenfant (1969) |
| Elephant seal *Mirounga angustirostris* | 4 | | 20.7 | 32.0 | | | Elsner (1969) |
| Weddell seal | 16 | | | 35.50 | | | Kooyman (1967) |
| *Leptonychotes weddelli* | 1 | 61.5 | 23.7 | 31.60 | | | Lenfant *et al.* (1970) |

* $O_2$ combining capacity = $O_2$ capacity/[Hb]

† Derived $O_2$ capacity = [Hb] x 1.34 (where 1.34 ml $O_2$ combines with 1 gm Hb, Torrance and Lenfant, 1969; Guyton, 1971)

‡ Values calculated by authors using [Hb] x 1.38

Table 3. Comparative packed cell volume (PCV) and hemoglobin concentration [Hb] for some terrestrial and marine mammals.

| Species | No. of specimens | PCV (%) | Hb (gm %) | Reference |
|---|---|---|---|---|
| Man | | 45.0 | 15.0 | Lenfant *et al.* (1970) |
| Dog | | 45.0 | 15.0 | Schalm *et al.* (1975) |
| Harbor seal | | 51.0 | 20.2 | Lenfant *et al.* (1970) |
| *Phoca vitulina* | 5 (captive) | 53.0 | 20.3 | Ferren (unpubl.) |
| Elephant seal *Mirounga angustirostris* | 7 | 63.5 | | Simpson *et al.* (1970) |
| Weddell seal *Leptonychotes weddelli* | 4 | 61.0 | 23.7 | Lenfant *et al.* (1969) |

Table 4. Comparative dive durations for some terrestrial and marine mammals.

| Species | Maximum Submersion (minutes) | Reference |
|---|---|---|
| Man | 1 (average swimmer)<br>2 (maximum) | Irving (1939)<br>Craig (1938) |
| Dog | 4.5 (forced submersion) | Bert (1870) |
| Ringed Seal<br>*Phoca hispida* | 21<br>21<br>23 | Freuchen (1935)<br>Parsons (1977)<br>Burns (personal communication) |
| Harbor seal<br>*Phoca vitulina* | 28<br>23 | Harrison and Tomlinson (1960)<br>Kerem and Elsner (1973b) |
| Elephant seal<br>*Mirounga angustirostris* | 40 | Van Citters *et al.* (1965) |
| Weddell seal<br>*Leptonychotes weddelli* | 55<br>45<br>60 | Lenfant *et al.* (1969)<br>Kooyman (1966a)<br>Elsner *et al.* (1970a) |

conclusions have substantiated the original paramount investigations and speculations published by Irving (1939) and Scholander (1940). As a consequence of these insights and the present state of knowledge, it is possible not only to investigate diving animals for adaptations to defend against submersion asphyxia but also to apply the knowledge of diving adaptations to examination of an animal in order to speculate on its possible capability for diving.

## The Consequence of Oxygen Depletion

Oxygen is needed to sustain life in animals whose metabolism is dependent on aerobic energy conversion. Maintenance of cellular integrity, both structural and functional, is based on availability of energy for the numerous vital molecular reactions. Although anaerobic energy conversion does occur within various tissues (and extensively within red blood corpuscles and active muscle tissue), the primary avenue of energy conversion within organisms is substrate oxidation with molecular oxygen serving as the terminal electron acceptor. Reduction of available oxygen leads to impairment of energy release and in severe oxygen depletion to death. In the brain, available bond energy is primarily in the form of ATP (adenosine triphosphate) and creatine phosphate. Nerve tissue has a high energy demand, for example, while the brain comprises a small percentage of the body weight, in humans it utilizes approximately 20 to 25% of the resting oxygen requirement (Best and Taylor, 1961). Nerve tissue depends on oxygen consumption because the anaerobic formation of energy-rich intermediates is insufficient for

the high obligatory metabolic needs. When presented with anoxia, the metabolic use of glucose terminates with production of lactate and oxidized co-factor nicotinamide adenine dinucleotide (which is used in the glyceraldehyde -3- phosphate dehydrogenase step of glycolysis). Regeneration of NAD+ in nerve tissue, however, is predominantly oxygen dependent and therefore a brief reaction as oxygen depletion develops and oxidizing capacity declines (Reichelt, 1968).

In man, dog and other animals lacking adaptations to defend against asphyxia, such as in apnea, tolerance of hypoxia is generally of short duration (2 to 4 min), before onset of anoxia and cerebral dysfunction.

Application of EEG (electroencephalogram) techniques has allowed investigators to determine the point of cerebral dysfunction. As oxygen content falls during hypoxia, a critical level is reached when cerebral function becomes stressed. At this point, a sudden and characteristic modification of the normal EEG pattern develops (Naquet and Fernandes-Guardiola, 1961). In terrestrial animals, this point coincides with the loss of consciousness (Cahn *et al.*, 1964). Kerem and Elsner (1973a), using the EEG technique, determined that an average time of 4.5 min lapsed before cerebral dysfunction took place in the dog during episodes of hypoxia. At this point, arterial oxygen partial pressure ($PaO_2$) was 14 mmHg and venous $O_2$ pressure ($PvO_2$) was 9 mmHg. Prior to this end point, no significant lactate concentration difference between arterial and venous blood took place in the brain, indicating virtual absence of anaerobiosis there. The measured duration compared favorably with the duration calculated (4.0 min), based on oxygen stores alone.

Similar experiments with Weddell and harbor seals indicated periods of asphyxia up to 65 min in the Weddell seal (Elsner *et al.*, 1970b) and 23 min in the restrained and submersed harbor seal (Kerem and Elsner, 1973b) before cerebral dysfunction. $PaO_2$ levels of 10 mmHg were reached before noticeable EEG alterations. Obligatory oxygen consumption ($\dot{V}O_2$) was observed to decrease several minutes before cerebral dysfunction, concurrent with significant (v-a) $C_{lact}$ differences in the brain, indicating conversion to partial anaerobiosis.

One can use heart rate as an indicator of $O_2$ depletion (as with the EEG recordings), since in the final minutes of EEG end point dives, heart rate sometimes increases. This phenomenon has been observed by researchers investigating terminal and EEG end-point dives (Elsner *et al.*, 1970b; Kerem and Elsner, 1973b). The increased heart rate may reflect release of medullary control centers that regulate cardiac function (Kerem and Elsner, 1973b).

## Physiological Adaptations as Defenses Against Asphyxiation

Apnea can be maintained until physiological function becomes impaired due to low oxygen pressure being delivered via the blood to vital organs, particularly the brain. In diving animals morphological adaptations and physiological mechanisms have evolved to defend against early and abrupt onset of impaired function. Some of these features have already been outlined; a more detailed discussion follows.

*Oxygen Stores*

To achieve prolonged submersion, sufficient oxygen must be available to meet the metabolic demands. Oxygen stores available to the tissues during apnea or diving are those contained within the blood, the body tissues and the lungs. In diving mammals, the largest portion of these stores is found in the circulating blood. The amount of oxygen contained within the blood is a function of the hemoglobin content, the packed red cell volume, and the total blood volume. Elevated blood oxygen stores provide a margin of additional oxygen to meet metabolic demands during apnea. The oxygen content of most tissues is generally small. Diving animals possess high concentrations of the muscle respiratory pigment myoglobin. Myoglobin binds with oxygen as does hemoglobin. Its function is to store and provide oxygen to muscle tissue. The high concentration of the pigment indicates a high capacity for oxygen storage in muscle tissue, a supply which could be utilized by muscle tissue during periods of reduced blood flow through the muscle.

This $O_2$ store, however, compares to only 25% of the $O_2$ within the circulating blood, as documented in the hooded seal, *Cystophora cristata*, and is rapidly exhausted during muscle activity and decreased muscle perfusion (Scholander, 1940). Oxygen stored in the lungs may add to the circulating blood. Packer *et al.* (1969) investigated oxygen stores and supply in the harbor seal. They found the total body exchangeable $O_2$ stores to be 0.79 liters (40 ml/Kg) of which the lung accounted for 14 ml/kg. This figure indicates a large portion of the $O_2$ stores are in the lung. However, these values reflect lung $O_2$ stores at functional

residual capacity or somewhat greater (during inspiration). Upon diving seals generally exhale, thus decreasing the available lung $O_2$ stores. This behavior has been observed in Weddell seals (Kooyman *et al.*, 1971), harbor seals (Harrison and Tomlinson, 1960), and ringed seals (personal observation). The lung volume does not provide an important oxygen depot to the animal during the dive (Kooyman, 1975). The major oxygen stores are contained within the circulating blood.

*Oxygen Economy*

One method for extending duration of apnea before oxygen stores are exhausted would be reduction of oxygen consumption. This would pose a problem in seals whose metabolism is high compared with that of terrestrial mammals. Metabolic rates 1.5 to 2.6 times greater than that of terrestrial mammals of corresponding weight (as predicted by Kleiber's 1961 equation) have been determined for sea lions (Matsuura and Whittow, 1973) and harbor seals (Miller and Irving, 1975; Miller *et al.*, 1976; Irving and Hart, 1957). Kooyman *et al.* (1973) reported high resting metabolic rates for adult Weddell seals and Scholander (1940) reported high metabolic rates for hooded and gray seals. Øritsland and Ronald (1975) reported the metabolic rate of the harp seal to decrease with age and approach values predicted for terrestrial mammals but clarify that disregarding the blubber, which is of low metabolic activity, the data would indicate a body core with high metabolism.

Although seals have large oxygen stores, the supply is curtailed by the high metabolic rate; Scholander (1940) calculated that the oxygen

stores available to the hooded seal would last 5 to 6 min during a dive. Experiments showed the seal capable of diving three times that long. Packer *et al.* (1969) calculated that the oxygen stores available to the harbor seal would be exhausted in 4 min of diving. Again, the harbor seal can dive five times longer than this.

There are cardiovascular responses to submersion and it is these features which permit economic use of the oxygen stores. This has been shown by pharmacologically abolishing diving bradycardia and peripheral vasoconstriction during submersion. Under such conditions seals are capable of diving approximately 4 min before being affected by critically low arterial oxygen levels (Kerem and Elsner, 1973b), durations which agree with the calculated time for exhausting oxygen stores. Evidently the extended duration is achievable as a direct consequence of the cardiovascular responses to diving.

*Cardiovascular Responses to Diving*

Upon submersion, cardiovascular adjustment occurs. The essential feature is vasoconstriction coupled with bradycardia. The result is a reduction in the vascular beds being perfused and a matched reduction in cardiac output in order to maintain blood pressure. Conservation of oxygen is thereby achieved. Circulation continues through the brain and myocardium supplying these vital tissues with the oxygen available. The elicitation and regulation of these cardiovascular responses is an interplay of reflexes including reflex apnea initiated by a trigeminal nerve reflex which results in bradycardia and vasoconstriction. These

responses are enhanced by arterial chemoreceptors sensitive to hypoxia (Daly *et al.*, 1977 and Elsner *et al.*, 1977). Expiration upon submersion also enhances bradycardia and vasoconstriction through a reduction in the activity of pulmonary stretch receptors. Reports by Angell-James and Daly (1972), Blix (1975a), Andersen (1963a,b) and Bron *et al.* (1966) clarify the nature of these responses and their elicitation.

## Morphological Adaptations

Associated with physiological adaptations are morphological modifications of the vascular system which assist this adjustment of blood flow. Three observable features are the large aortic bulb, the voluminous inferior vena cava and hepatic sinus and the diaphragmic or caval sphincter.

Investigators have examined these morphological adaptations associated with the function of the dive response. In the dive, the large, bulbous and elastic root of the aorta is believed to receive the entire systolic ejection and slowly meter out the volume to the arterial circuit during the long diastolic interval, thereby maintaining a steady pressure and arterial flow (Elsner, 1972). Harrison and Tomlinson (1956) reported that constriction of the caval sphincter during submersion retards venous return via the inferior vena cava, and causes distension of the heptic venous sinus. Slow release of this blood store through the sphincter, towards the heart, thus into arterial circulation, may provide a slow metering of partially oxygenated blood into the oxygen depleted circuit late in the dive (Elsner *et al.*, 1964; Elsner *et al.*, 1971).

Physiological Adaptation and Ecological Implications of Diving

Seals have evolved adaptations to defend against the rapid onset of physiological complications due to diving asphyxia. These adaptations include increased $O_2$ storage capability and selective and differential use of the oxygen. In this manner vital organs are protected from $O_2$ depletion.

This degree of adaptation, however, does not appear to be the same in all species, as evidenced by their different diving capabilities. Phocid seals are longer divers than otariid seals. Maximum diving durations achieved by phocids range from more than 20 min for the harbor seal (Harrison and Tomlinson, 1956; Harrison and Tomlinson, 1960; Kerem and Elsner, 1973b) to 60 min for the Weddell seal (Elsner *et al.*, 1970a). In comparison, otariid seals, for example the northern fur seal, can dive for only 5 min (Irving *et al.*, 1963). Differences in adaptation are to be found accountable for these observations in the different seal families. However, when comparing only phocid seals, differences in diving capability are also noted between phocid species. This observation raises such questions as: are the physiological adaptations different, for instance, $O_2$ storage capacity, greater tolerance to reduced levels of oxygen, or different selective degrees of vasoconstriction? If a larger seal has a greater capacity to store more oxygen, then body size might correlate with capacity for long diving.

Differences in diving ability also raised questions concerning behavioral adaptation to the environment. Do seals living in similar environments have comparable dive durations? To speculate on which

behaviors are more fundamentally associated with dive duration is difficult, if not impossible. Feeding excursions are most certainly an important factor for which such adaptations have developed. So too, social interactions, escape from predators, avoiding obstacles (such as ice floes), and even sleeping or resting periods have evolved in concert with physiological adaptations.

With these variables and questions in mind, it is important to compare the fundamentals of environment, behavior, and diving ability of the two species that have been most studied. These are the Weddell seal and the harbor seal; the elephant seal is also included for discussion where data are available. The physiological adaptations including large blood volume, elevated PCV and the responses to submersion including abrupt and profound bradycardia and selective redistribution of blood flow have been documented in these species (Lenfant *et al.*, 1969, 1970; Elsner *et al.*, 1966). Because they reside in very different environments, detailed comparison of their physiological and diving characteristics should provide a basis for predicting the physiological adaptations and diving capability of other species that inhabit comparable environments. The ringed seal, *Phoca hispida*, has been regarded as the Arctic ecological counterpart of the Antarctic Weddell seal (Stirling 1969b, 1977). To focus on diving capability and its possible adaptive relationship to ice covered habitats, the ringed seal was investigated in this study and compared with the Weddell seal. Since the harbor seal is much smaller than the Weddell and similar in size to the ringed seal, it provides a basis for comparing diving

capability as a function of body size. The elephant seal, several times larger than the Weddell and other seals aids this body size - dive duration discussion. Harbor and elephant seals reside in the temperate zone and not in association with continuous shore-fast ice, as are the ringed and Weddell seals (Scheffer, 1958; Shaughnessy and Fay, 1977).

The Weddell seal and ringed seal are the only two species of phocids to inhabit shore-fast ice zones, both having developed unique behavior to maintain breathing holes through ice (Stirling, 1969a; Smith and Stirling, 1975). Weddell and elephant seals are divers of exceptionally long duration (Table 4). The harbor seal can dive for extended periods, but at most less than half as long as a Weddell seal. Freuchen (1935) observed a ringed seal dive for 21 min. Parsons (1977) observed a captive ringed seal dive for 20.7 min. John Burns (personal communication) observed a ringed seal resting (as if sleeping) on the water surface, with head submerged for 23 min.

From examination of EEG diving records and physiological data of Weddell and harbor seals, parallel adaptations are evident. For example, compared with terrestrial mammals, both seals have high oxygen storage capability and both seals exhibit cardiovascular responses to submersion. However, these two species differ widely in their maximal dive duration: the Weddell seal can submerge for periods two to three times longer than that of the harbor seal. Is this a consequence of a differential degree of physiological adaptation or related to physical differences (such as size) between these two species?

Kooyman (1966a) suggests that the dives of Weddell seals which exceeded 20 min "... seemed to be exploratory; the seals were probably searching for breathing holes" (p. 1554). Hunting dives were deeper and shorter, generally not exceeding 15 min (Kooyman, 1967). It is vital that those seals associated with ice, particularly shore-fast ice, must have access to open leads, or holes for breathing. Capability for dives of long duration permits searching for breathing holes. DeVries and Wohlschlag (1964) suggested that "Weddell seals possess a well-developed navigational system which enables them to swim long distances under thick ice shelves where light and breathing holes are limited" (p. 292). That Weddell seals have been observed in tidal cracks tens of kilometers shoreward from the edge of the Ross Ice Shelf supports this contention (DeVries and Wohlschlag, 1964). Lenfant *et al.* (1970) also suggests that because this species remains in an area of continuous shore-fast ice, it appears to have developed the ability to exploit and tolerate the under-ice environment, indicating both orientation and diving ability (depth and duration) to be the important physiological adaptations.

The ringed seal has a wide range throughout the regions of seasonal and permanent pack ice of the Arctic. Adult ringed seals occupy areas of shore-fast ice during the breeding season. Only the Weddell seal occupies such a comparable range but in the Antarctic (Fig. 1). So nearly identical are the behavior and distribution of the Weddell and ringed seals within the fast ice habitat that Stirling (1969b, 1977) has called these species 'ecological counterparts' presenting examples of

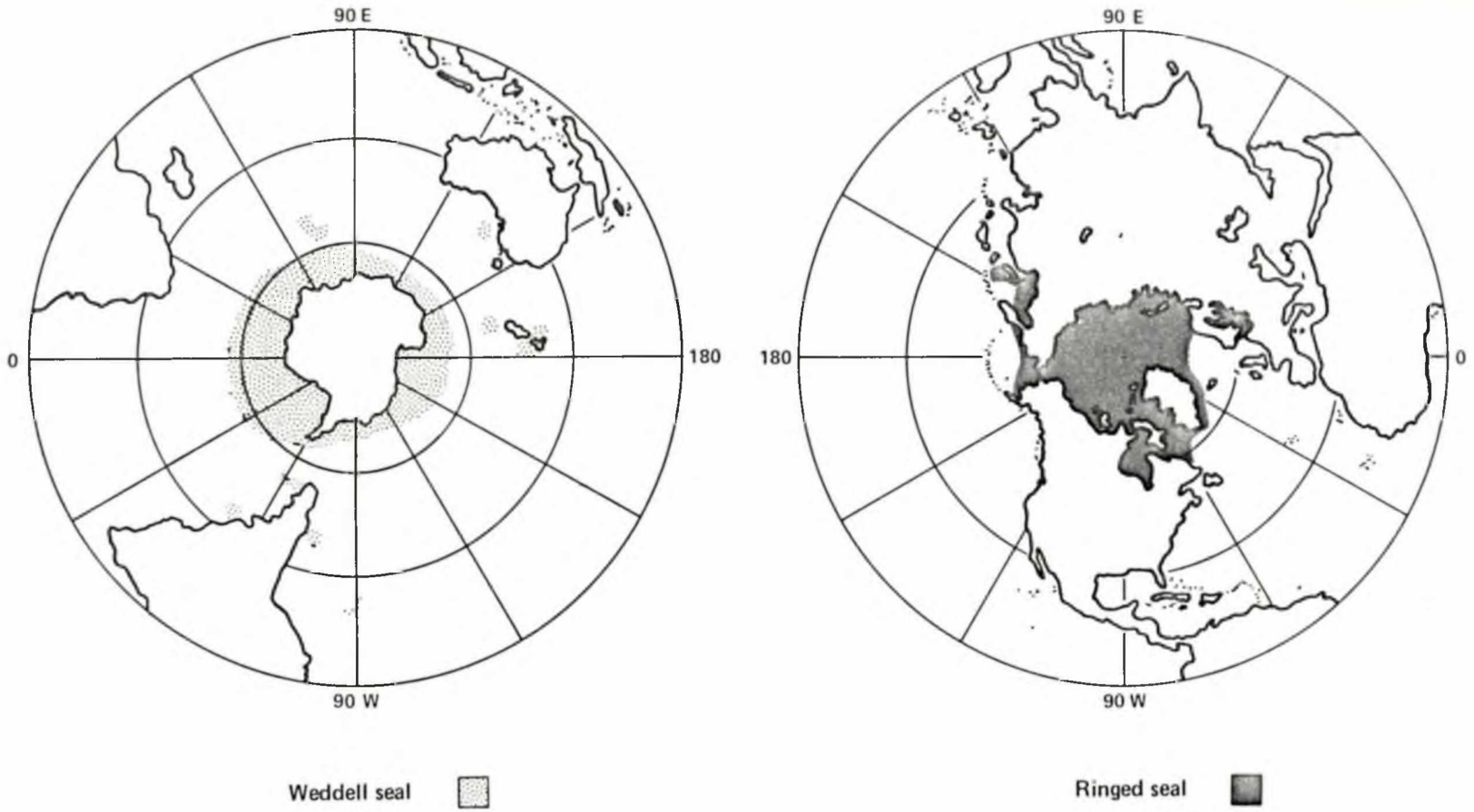


Figure 1. Distributions of the Weddell and Ringed Seal in the Polar Regions of the Antarctic and the Arctic (after Scheffer, 1958, pp. 96 and 124).

parallel evolution (Table 5). Weddell seals are 5 to 8 times larger than ringed seals; they also dive deeper and longer than ringed seals. Adults of both species generally occupy stable, shore-fast ice and both species exhibit agonistic behavior at breathing holes, particularly during the breeding season. Kooyman (1967) suggests: "The aggressive behavior of *Leptonychotes* may play an important role in the distribution of animals at the scattered diving holes. The individual that has the ability to swim out under the ice and find an unoccupied hole has improved his chances survival" (p. 257). Stirling and McEwan (1975) report intraspecific agonistic behavior of ringed seals, particularly during the breeding season and to such an extent that "... dominant seals probably reduce the sub-ice movements of subadults between breathing holes, and possibly precludes maintenance of breathing holes by subadults in closely adjacent areas... dominant seals may actually exclude some younger individuals from the water long enough for their breathing holes to freeze over".

Previous discussion implies the long diving capability of the Weddell seal is an adaptation to the shore-fast ice habitat. An alternative speculation is that the observed diving differences are attributable to the size of the animal i.e. greater oxygen storage capacity relative to the mass of vital organs utilizing this oxygen during the dive. The organs perfused during diving are the heart, brain and lungs, the brain being the most sensitive to hypoxia. If large pinnipeds have a small brain mass relative to the body mass, then Weddell seals would have a relatively smaller brain/body mass proportion than harbor and

Table 5. Comparison of Weddell seal to ringed seal: biology and behavior.

| | Weddell seal | Ringed seal |
|---|---|---|
| Size | 400 kg (Elsner, personal communication) | 90 kg (Burns and Eley, 1976) |
| Food | Fishes, mostly nototheniid fishes reaching 25 kg, and cephalopods (Dearborn, 1965) | Planktonic, nektonic and benthic crustaceans and fishes (mostly arctic cod) (Burns and Eley, 1976) |
| Maximal dive depth | 600 m (Kooyman, 1966) | 90 m (McLaren, 1958) |
| Dive duration | 43.3 min (Kooyman, 1970a)<br>60 min (Elsner *et al.*, 1970a) | 21 min (Freuchen, 1935)<br>21 min (Parsons, 1977)<br>23 min (Burns, unpublished) |
| Maintenance of breathing holes | Abrades ice with teeth | Abrades ice with claws on fore flippers |
| Physical conditions of habitat | Immature animals are found in unstable moving ice; adults are found in stable, shore-fast ice | Immature seals occupy the unstable, moving ice; adults are found in stable shore-fast ice |
| Behavior | Both males and females defend aquatic territories during breeding season Stirling, 1969b) | Adults appear to defend aquatic territories during breeding season (Stirling and McEwan, 1975) |

ringed seals. With similar blood volume and oxygen capacity per kilogram of tissue, the Weddell seal would be expected to consume its oxygen stores during a dive at a slower rate than the harbor and ringed seals and be able to endure longer submersion. Cerebral impairment (detected by EEG patterns) has been shown to occur when arterial oxygen pressure falls to 10 mmHg in both the harbor seal (Kerem and Elsner, 1973b) and the Weddell seal (Elsner *et al.*, 1970b). Although the $PaO_2$ was lowered to equivalent values during these experimental dives, the harbor seal experienced this low value after average dive durations of 18 min (maximum of 23 min) and the Weddell seal after average episodes of 50 min. These facts indicate that the Weddell seal may indeed consume its oxygen store more slowly.

The ringed seal is the smallest of the phocid seals, in which case it could be expected to have the largest brain/body mass proportion and, therefore, the shortest diving duration, given that its $O_2$ storage/kg of tissue is comparable to Weddell and harbor seals. Diving ability and $O_2$ storage of the ringed seal have not been well documented. Hence, this study was designed to measure those parameters as a test of the above hypothesis.

## OBJECTIVES

The objectives of this study are:

A. To determine the diving capability and associated physiological and morphological adaptions of the ringed seal;

B. To use the results as a comparison with data for Weddell, elephant and harbor seals;

C. To evaluate the predicted relationships between diving capability and habitat *versus* brain/body size.

## METHODS

### Maintenance of Captive Ringed Seals

In June of 1975, two ringed seal pups, a female and a male (seals #2 and #3), and a one-year old female (seal #1) were captured on sea ice in the Bering Sea in the vicinity of Gambell, St. Lawrence Island, Alaska. The seals were flown to the Institute of Arctic Biology at the University of Alaska, Fairbanks. On arrival the two pups weighed 8.4 kg and 8.3 kg, while the one-year old weighed 11.5 kg.

The animals were maintained together in an outdoor pen (1.5m x 4.3m), in which they had access to 2 small pools (1.5m x 0.6m x 0.5m deep) with running fresh water and a haul-out platform (0.6m x 1.2m) at the side of the pools. The range of air temperatures in the pens was from -46°C in winter to +33°C in summer. The pools were kept from freezing during winter by increasing the flow of water, which also kept the water temperature above 5°C in winter and below 22°C in summer.

Once per day, freshly thawed herring (*Clupea harengus*) were fed to these seals. Small herring (12 cm long) were fed whole; larger herring were cut into pieces about 4 cm long. One multiple vitamin tablet for general vitamin replacement, one 2.25 mg NaCl tablet for dietary electrolytes (Hubbard, 1969), one vitamin $B_1$ tablet (100 mg) to thwart thiamin

deficiency (Geraci, 1972), and one vitamin E capsule (200 units) for diets high in polyunsaturated fats (Keyes, 1968) were given each seal daily.

## Oxygen Stores

The packed cell volume (PCV), hemoglobin concentration [Hb], oxygen capacity of the blood (volume of $O_2$/ml whole blood), and total circulating blood volume were measured as follows.

### *Packed Cell Volume (PCV)*

PCV's determined by the microhematocrit method are presented as percent by volume RBC per ml of whole blood. Blood was sampled using 18 gauge 1-1/2 inch sterilized needles and 5 ml syringes previously treated with heparin (5000 U.S.P. units per ml). Heparin was drawn into the syringe and forcefully expelled, leaving a film in the syringe. The seals were restrained and the needle guided through the skin and fat between the vertebrae of the thoracic or lumbar region and into the extradural intervertebral vein (EDIV). PCV determinations were conducted within several minutes of sampling by microhematocrit centrifugation.

### *Hemoglobin Concentration*

Hemoglobin concentration is expressed as mg percent by weight of hemoglobin per ml of whole blood. The red corpuscles were first lysed to liberate the hemoglobin molecules. The ferrous iron was then oxidized

to the ferric form to get methemoglobin, which was allowed to bind cyanide ions, forming cyanmethemoglobin. The concentration of cyanmethemoglobin was determined via spectrophotometric analysis and plotting the absorbancy values (at 540 nm) on a standard curve prepared by testing certified standard solutions. The reagents employed were HYCEL cyanmethemoglobin reagents, certified standards and hemoglobin controls. A Beckman quartz spectrophotometer was used to determine the cyanmethemoglobin absorbancy.

*Oxygen Capacity*

The oxygen capacity of whole blood from the EDIV was determined by the Van Slyke volumetric method. A 2 ml sample was injected into the mixing chamber of the Van Slyke apparatus, exposed to and allowed to equilibrate with room air. Alkaline ferricyanide was used to liberate the gases from the hemoglobin molecules. The gases were then vacuum extracted from the solution and the volume of oxygen determined by selective absorption of the oxygen with a sodium hyposulfite solution while noting the volume change of the gases in the microgas burrette. The obtained $O_2$ volume was then corrected for ambient temperature and pressure (Van Slyke, 1932).

*Blood Volume*

Total blood volume is expressed as ml of blood per kg total body mass (TBM) and lean body mass (LBM). Total blood volume was determined indirectly by radioisotope dilution (Hlad and Tanz, 1958; Ridgway and

Johnston, 1966; Simpson *et al.*, 1970). Human serum albumin labelled with $^{131}I$ was obtained from Abbott Radio-Pharmaceutical with activities of 1 mc/3 ml. One ml portions of the radioactive isotope were prepared for injection. The activity of each aliquot was 30 μc/ml. Standard solutions were prepared by mixing 1 ml aliquot of the isotope with 1 liter of distilled water.

Blood was sampled from the EDIV prior to injection for background activity determination. Seals were restrained and the experimental doses injected by syringe directly into the EDIV. Blood samples were taken at 10, 20 and 30 minutes post injection. Equilibration of the isotope was generally complete within 10 minutes. The serial sampling procedure was followed to estimate error and assure equilibration of the isotope within the animal. Sample aliquots were counted in a Searle 1195 Series Automatic Gamma Counting System. Activities of the aliquots from the 10, 20 and 30 minute samples were averaged and corrected for background activity. Total blood volume was calculated as:

$$\text{TBV (ml)} = \frac{\text{(cpm/ml standard) x [dilution volume (ml) standard]}}{\text{cpm/ml of whole blood}}$$

Concurrent total body water determinations were performed by the tritiated-water method in order to calculate lean body mass (Holleman and Dieterick, 1973). Blood samples at 2, 3, and 4 hours post injection were obtained and vacuum distilled. One ml aliquots were taken from the distillate and pipetted into 5 ml of scintillation fluid composed of 700 ml Triton X (Packard Chemicals), plus 300 ml toluene, plus flours (4 g PPO/1 + 50 mg POPOP/1). PPO and POPOP indicate 2,5 diphenyloxazole and 1,4 -BIS [2- (4- methyl -5- phenyloxazolyl)] benzene, respectively.

The activities of the samples were then counted in a liquid scintillation detection system. The activities of the aliquots from the 2, 3, and 4 hour samples were averaged and corrected for background activity. Total body water (TBW) was calculated as:

$$TBW = \frac{\text{(cpm/ml standard) x [dilution volume (ml) standard]}}{\text{cpm/ml of whole blood}}$$

Pace and Rathbun (1945) showed that 73.2% of lean tissue in various animals is water. To obtain an estimate of the LBM, therefore, I multiplied the total body water value by 0.732. During this investigation, Stirling and McEwan (1975) determined that ringed seal lean tissue was 71.1% water in close agreement with Pace and Rathbun. This value (LBM) subtracted from the total body mass indicates the fat content of the TBM. The LBM allows calculation of the oxygen stores available to the metabolically active tissues of the animal, i.e. excluding the fat.

## Morphology

The circulatory anatomy of the ringed seal was examined and compared with that of other phocids. This involved dissecting three ringed seal carcasses and comparing their anatomical features with those of other phocids as described by Harrison and Tomlinson (1956). Five harbor seal carcasses also were examined by dissection.

## Dive Duration and Responses

Experimental dives were conducted as forced submersions. The seals were restrained in a canvas harness mounted to a board. The board and

seal were tipped forward until complete head submersion was obtained. Heart rate was monitored with a Sanborn 320 Dual Channel DC Amplifier-Recorder. Copper disc surface electrodes were placed over shaved patches on the dorsal aspect of the thoracic region of the restrained animal. A Biocom Bioamplifier (Model 2122) was used to increase the ECG signal transmitted to the amplifier-recorder. Forced dives were initially conducted to durations of 1-4 min. These short dives were conducted to accustom the seals to restraint and forced submersion. Subsequent dives were conducted for 8-12 min as further training prior to maximal submersion durations. Maximal dive duration was indicated by physiological impairment (abrupt increase in heart rate and/or erratic cardiac activity). Electrocardiograms were obtained during all dives.

### Brain Weights

The brain was removed from 2 experimental seals after death and weighed. Two additional brain weights together with body weights of the same animals were obtained from the Alaska Department of Fish and Game.

## RESULTS

### Maintenance of Captive Ringed Seals

The amount of herring fed to the seals (Fig. 2) was based initially on each seal's apparent appetite. Following the death of seal #3 from

pneumonia, daily food allotments were reduced in order to lower the weight of the seals, as the obesity of seal #3 was suspected to have contributed to the death of that animal. Weights of the three seals (Fig. 3) compared with food intake (Fig. 2) did not coincide.

Figures 2 & 3 also indicate the time of death for each animal. Seal #3 died from pneumonia; seal #2 died during surgery to expose the femoral artery following administration of 17 mg valium (IM injection) and 10 cc 2% xylocain (local); seal #1 succumbed to apparent accidental asphyxiation during an experimental dive. The physical data at death for each animal are presented in Table 6 and compared with weight data collected from wild ringed seals.

## Oxygen Stores

The packed red cell volume (PCV), the hemoglobin concentration [Hb], the oxygen capacity of the blood, and the total blood volume (Table 7) are indicative of oxygen storage capability. Mean total blood oxygen storage capacity was 0.82 liters of oxygen, or 70 ml $O_2$/kg LBM.

## Morphology

The bulbous aorta, the enlarged posterior vena cava and hepatic sinus and the caval sphincter were found to be present in the 3 ringed seals dissected (Figs. 4, 5 and 6). The elastic and enlarged root of the aorta can contain approximately the entire stroke volume of the heart. Distending with the systolic ejection, this structure stores kinetic energy for metering the blood into the arterial circuit during

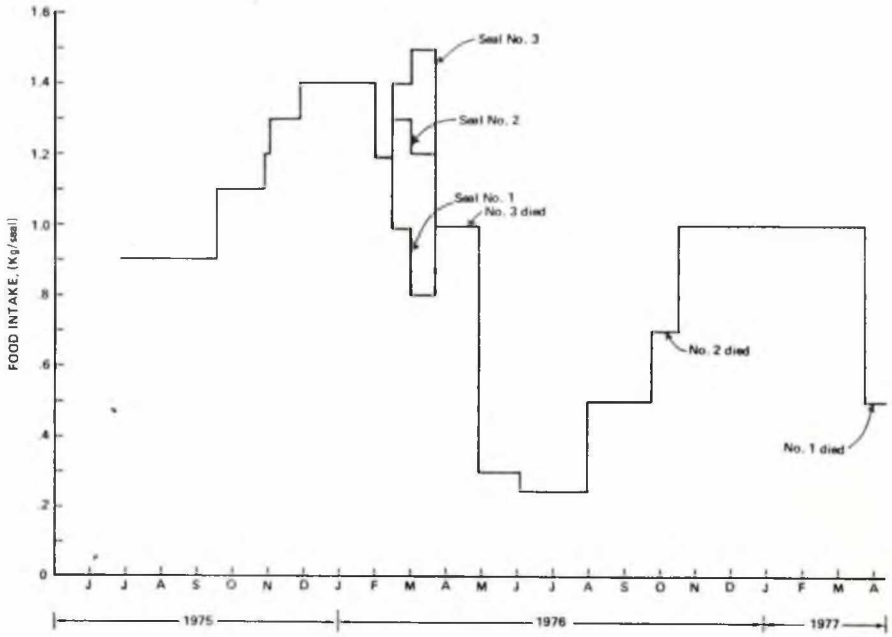


Figure 2. Food intake by ringed seals during period of captivity.

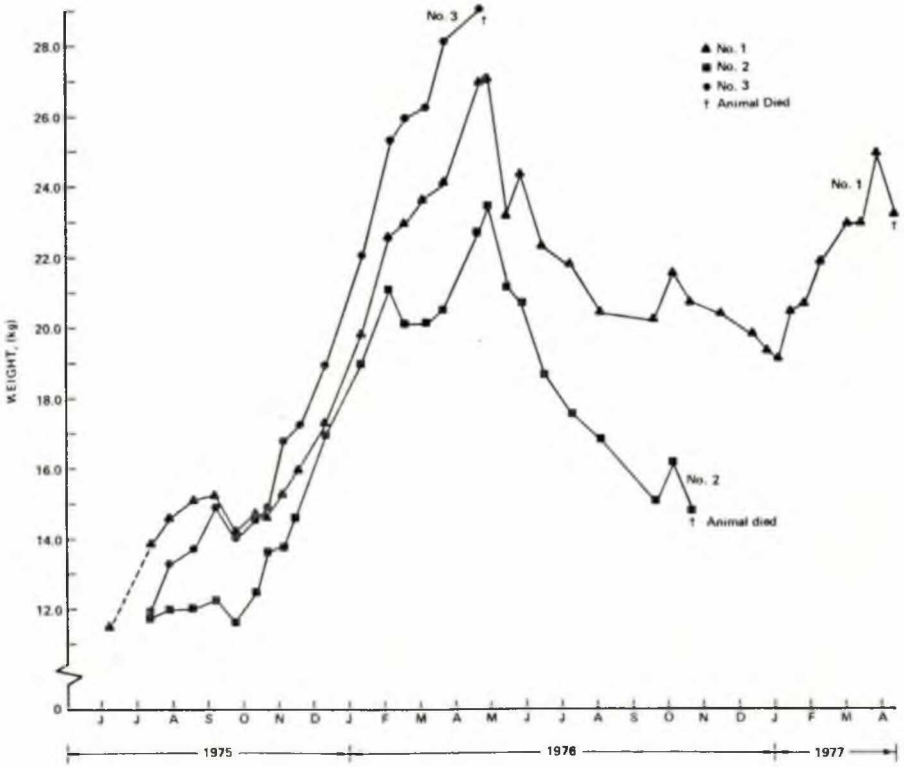


Figure 3. Body weights of ringed seals during captivity.

Table 6. Total body mass (TBM) of experimental and wild ringed seals at death.

| Experimental seals | | | | | Wild seals* | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Animal | Sex | Age (yrs) | Date of death | TBM (kg) | Animal (n) | Sex | Age (yrs) | Date collected | Mean TBM |
| 1 | ♀ | 3 | Apr 77 | 23.2 | 6 | ♀ | 3 | May 76 | 24.5 |
| 2 | ♀ | 1.5 | Oct 75 | 14.8† | 6 | ♀ | 1.5 | May 76 | 20.5 |
| 3 | ♂ | 1 | Apr 76 | 28.4 | 5 | ♂ | 1 | May 76 | 22.3 |

* Data from wild seals provided by Alaska Department of Fish and Game, Fairbanks, Alaska from specimens collected near Diomede Island, Nunivak Island and St. Lawrence Island.

† Weight of subject was 21.1 kg in May 1976.

Table 7. Blood parameters of the three ringed seals used in experiments.

| Blood Parameters | Sample (n) | Range | Mean ± S.D. |
|---|---|---|---|
| Measured Values | | | |
| Total blood volume (liters) | 7 | 2.19 - 3.31 | 2.67 ± 0.35 |
| Total blood volume ml/kg TBM | 7 | 122 - 192 | 151 ± 26.0 |
| Total blood volume ml/kg LBM | 7 | 208 - 314 | 234 ± 35.5 |
| PCV (% whole blood) | 41 | 42.0 - 61.3 | 53.2 ± 4.04 |
| Hb conc. (gm%) | 33 | 19.7 - 26.6 | 23.7 ± 1.82 |
| $O_2$ capacity (ml/100 ml whole blood) | 4 | 29.20 - 32.02 | 30.7 ± 1.64 |
| Calculated Values | | | |
| $O_2$ combining capacity = ($O_2$ capacity/[Hb]) | | | 1.3 |
| Derived $O_2$ capacity = [Hb] x 1.34 | | | 31.7 |

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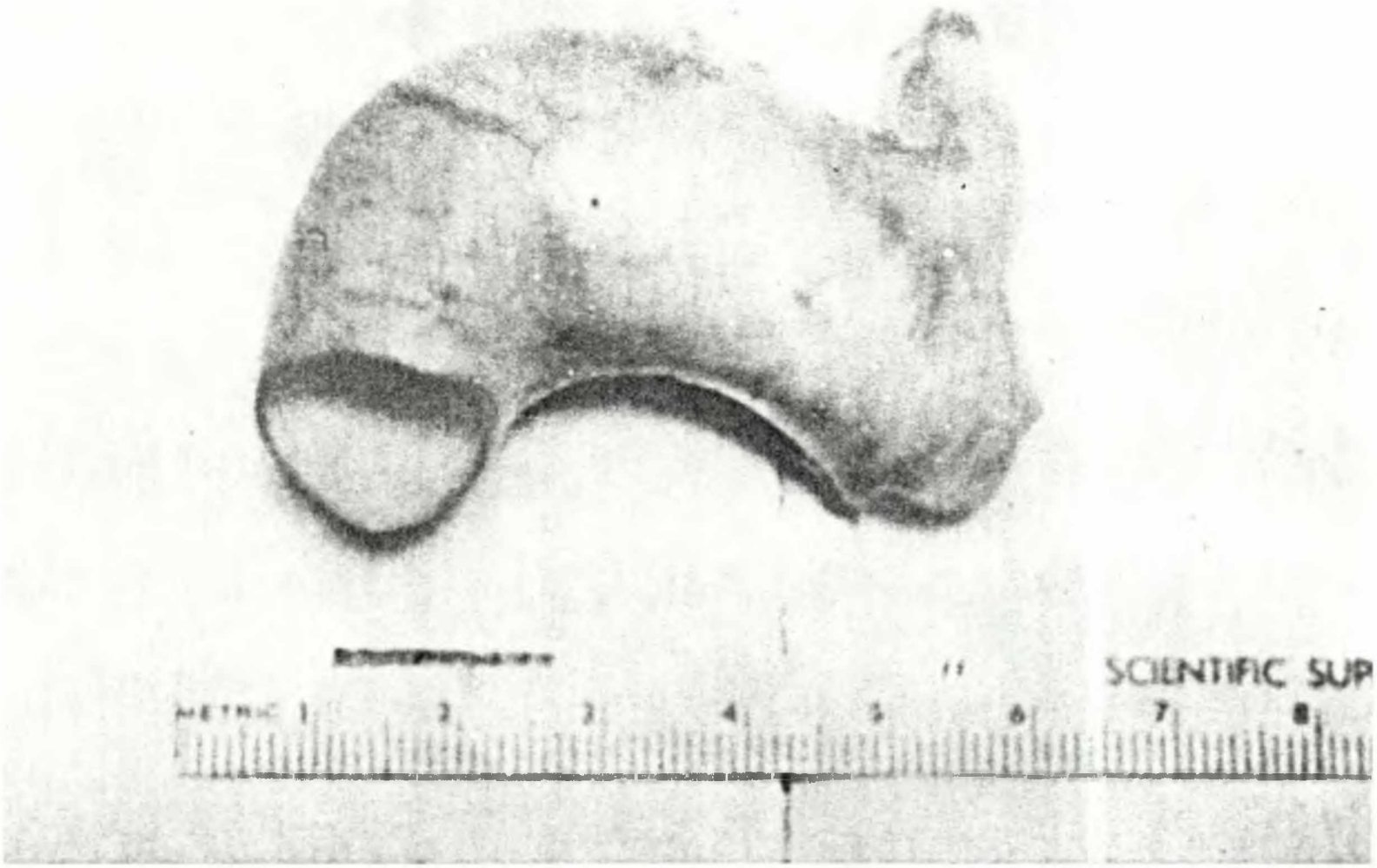


Figure 4. Photograph of bulbous aorta removed from yearling ringed seal.

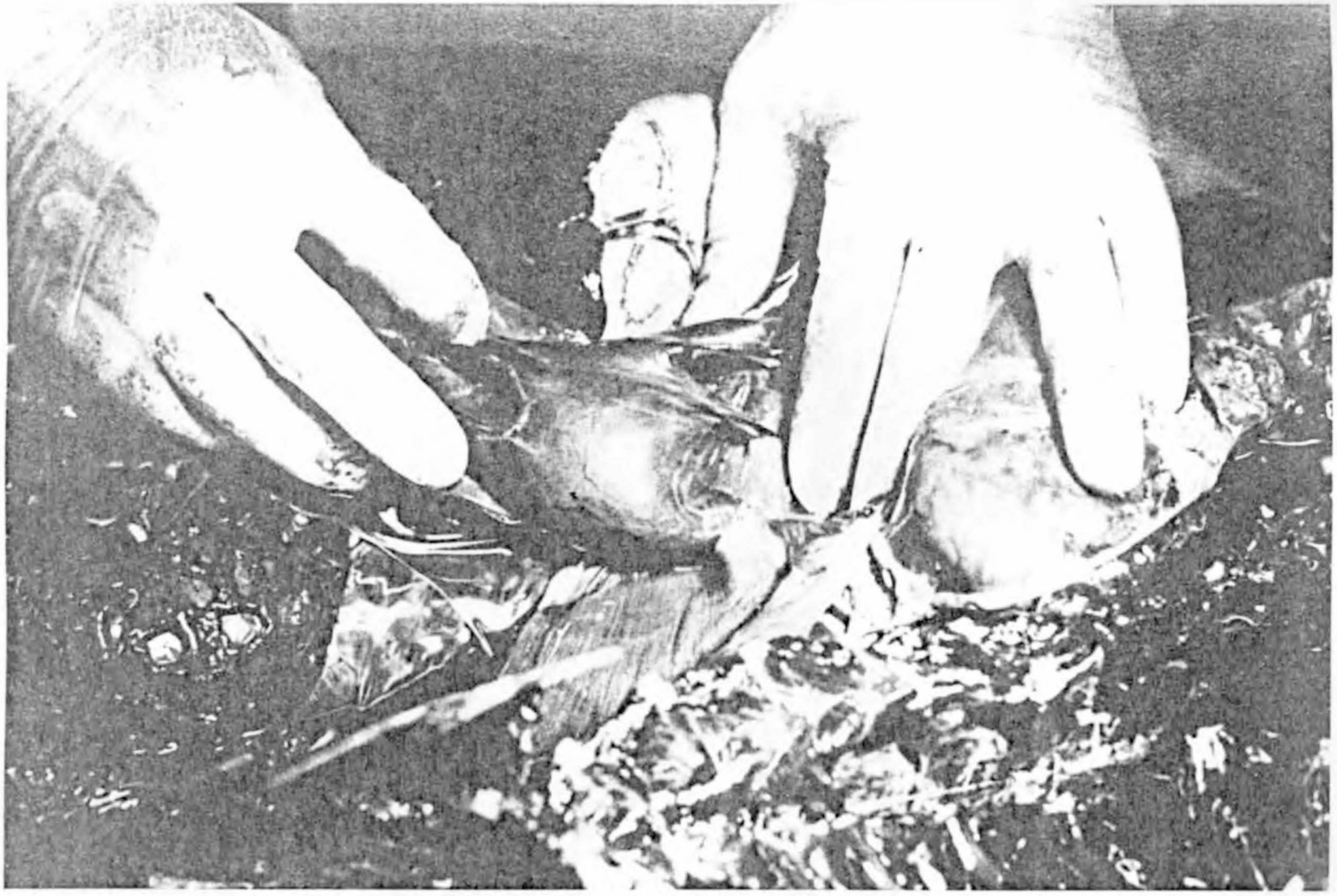

Figure 5. Photograph of inferior vena cava distended with blood.

Figure 6. Photograph of the diaphragm sphincter.

diastolic intervals thus contributing to the maintenance of arterial blood pressure. A large blood volume can be contained within the hepatic sinus and vena cava. For example, in the elephant seal, as much as 1/5 of the entire blood volume can be contained within this structure. This volume of blood may function as an oxygen reservoir during diving. Constriction of the diaphragmic sphincter sequesters blood in the hepatic sinus and vena cava.

Heart Rate During Dive

A total of 53 forced dives were conducted with ringed seals. A consistent pattern of heart rate alteration was observed in the experimental ringed seals upon submersion (Fig. 7). Often, the heart rate was elevated prior to submersion, then was followed by abrupt bradycardia. The lowest heart rates, down to 10-15% of pre-dive, were achieved immediately or within one minute into the diving episode. Maintained bradycardia, evidenced by the ECG record, was immediately ended at the dive's termination. Post-dive tachycardia was evident.

At the outset of this study, the possibility of training the seals to perform unrestrained dives was considered along with forced submersion. The response of seals to unrestrained submersion has been examined by several investigators (Murdaugh *et al.*, 1961b; Elsner, 1965; Casson and Ronald, 1975). The physiological responses to such dives probably correspond closely to those under natural conditions. Because it was the physiological capability of the biological system that was the primary concern in this study, forced dives with proper monitoring

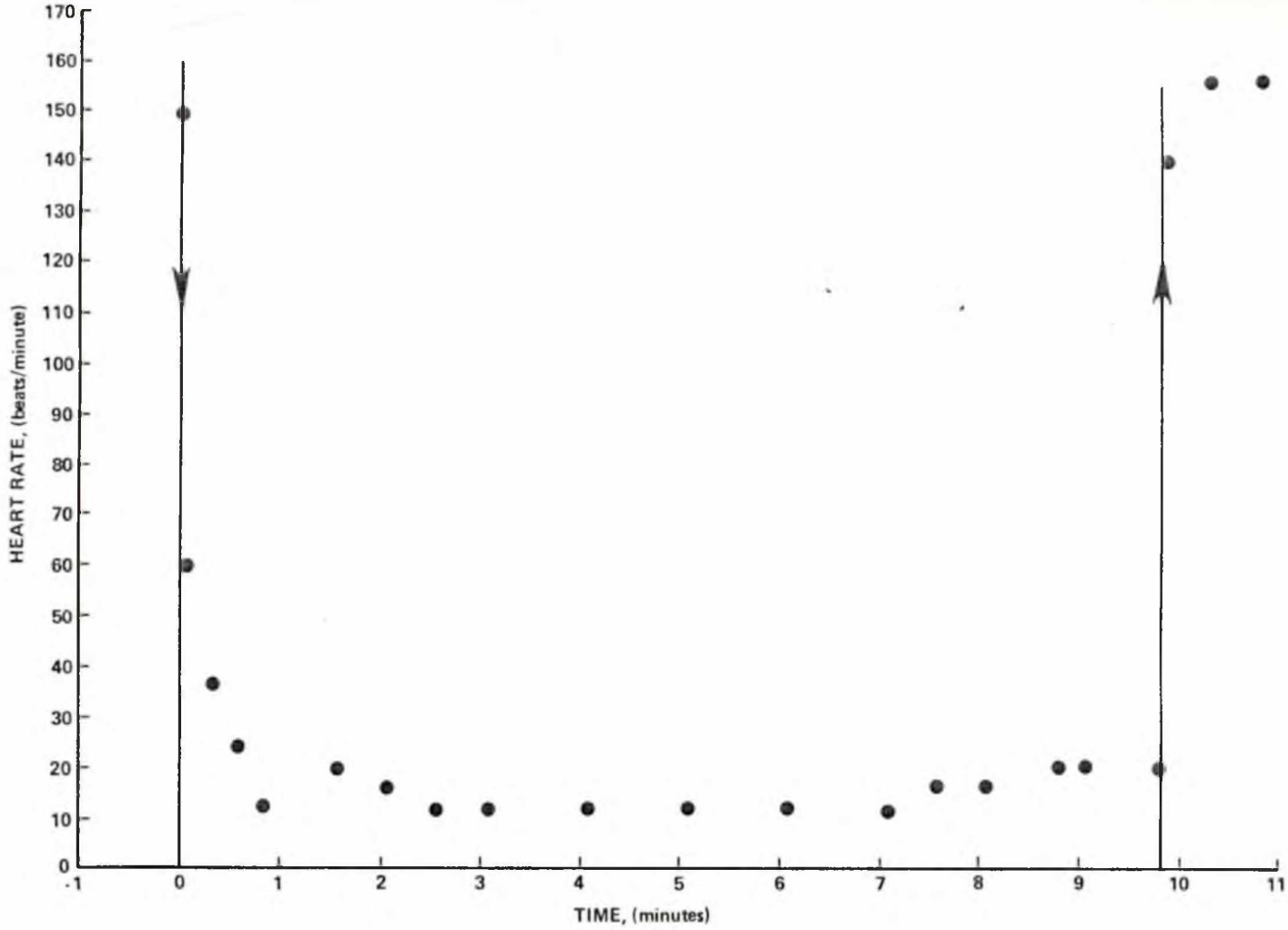


Figure 7. Typical heart rate during forced dive of ringed seal #2.

were more appropriate, since the animal could be stressed to maximal limit of its physiological adaptation. Maximal stress probably happens rarely during a free, unrestrained dive.

Prior to the forced diving experiments, I trained two ringed seals to immerse their heads in a pail of water on command. Under these conditions, their heart rate usually dropped to 40 to 60 beats per min, which was similar to that observed during periods of apneic bradycardia. At no time could I encourage the seals to remain under water for more than 4 min. Following such episodes, each seal would raise its head and hyperventilate, as if having exhausted its oxygen supply. Although moderate bradycardia was exhibited during immersion, the seals' behavior following emergence suggested that full alteration of blood flow did not take place as in the forced dives. This was not a unique observation (cf. Scholander, 1940; Elsner, 1965).

The longest forced dive for a restrained ringed seal was terminated by the investigator at 17.85 min (Fig. 8). Abrupt, steady bradycardia occurred throughout the dive until 15 seconds before its end. At that point, erratic heart beats were interpreted as indication of physiological stress and possible impairment of medullary centers regulating heart function. A very high tachycardia and respiratory rate took place following the dive (Fig. 9). In an experimental dive eight days later with this same animal, heart rate and visual signs of stress (struggling and nostril opening) were observed 30 seconds before termination of the dive at 16.18 min (Figs. 10 and 11). Post diving hyperventilation and tachycardia did not occur; there was no spontaneous

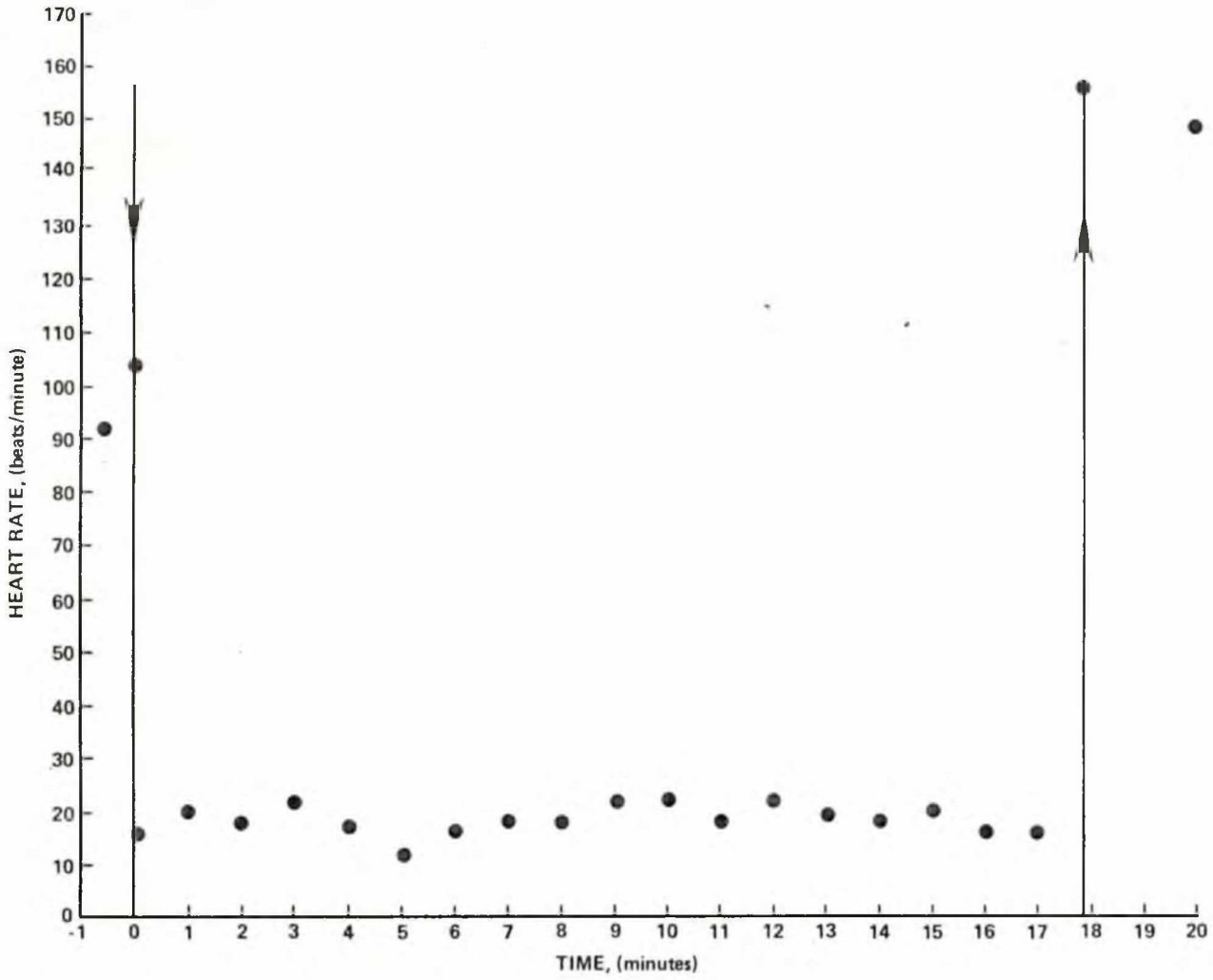


Figure 8. Heart rate during maximal forced dive (17.85 min) of ringed seal #1.

A. 15 seconds into dive. Heart rate 24 beats/ minute.

B. 15 minutes into dive. Heart rate 12 beats/ minute.

C. 17:30 minutes into dive through end of dive, note erratic heart beats and post-diving tachycardia.

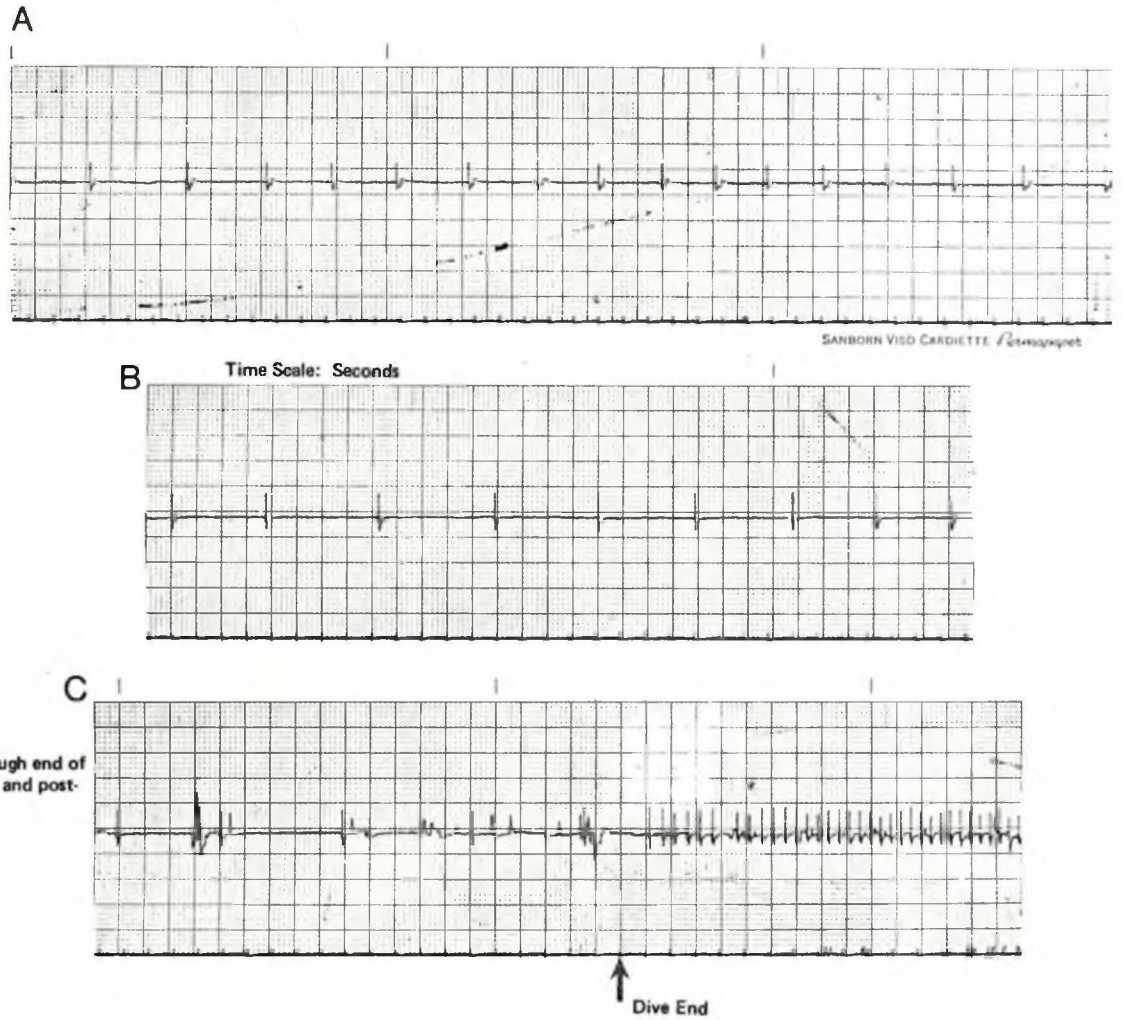


Figure 9. Initial and late segments of the ECG record of dive represented in Figure 8.

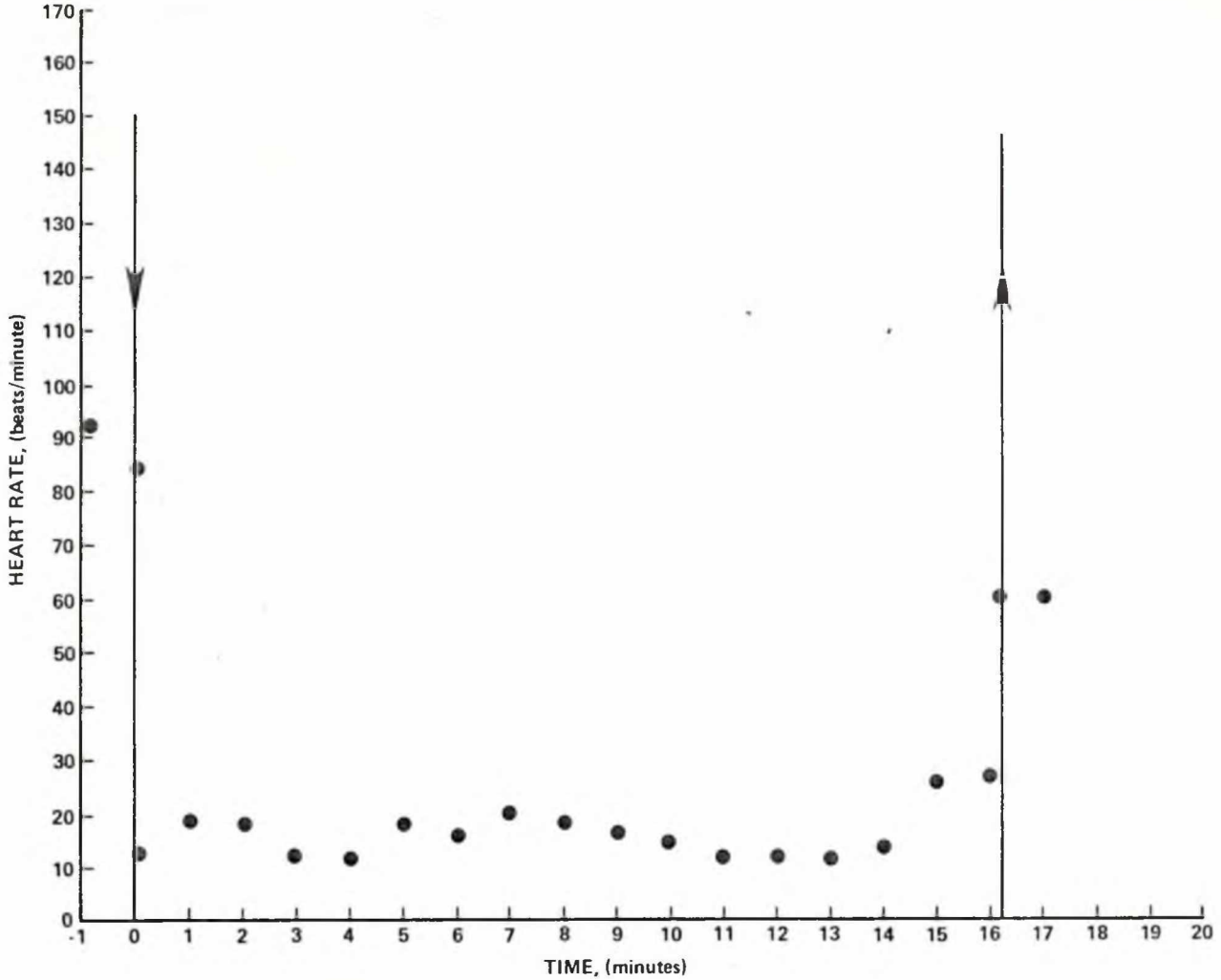


Figure 10. Heart rate during lethal (16.18 min) forced dive of ringed seal #1.

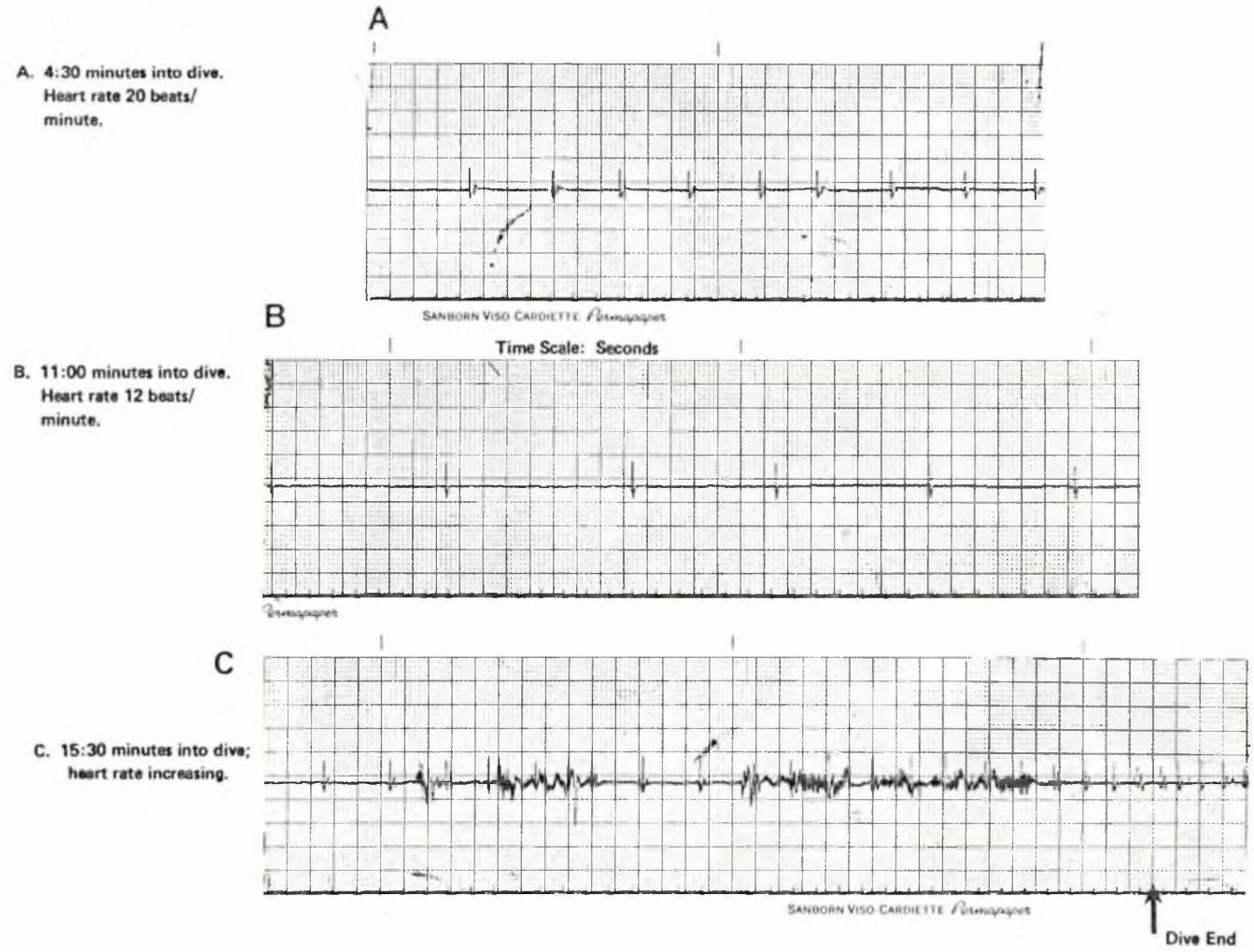


Figure 11. Initial and late segments of the ECG record of dive represented in Figure 10.

respiration. Heart rate rose only to levels comparable to apneic bradycardia (40 to 60 beats per min). Resuscitation was attempted with tracheal intubation, artificial respiration and atropine-chloride ventricular injection, all without success. Attempts to revive this animal were ended after 60 min. Post mortem dissection and histological analysis indicated severe congestion, edema and hemorrhage of the lungs. These signs, not indicative of drowning, are more typical of cardiopulmonary collapse, as might be observed in asphyxiation (R. Dieterich, personal communication).

If indeed this seal died from asphyxiation, it is not likely that it was directly due to struggling or other activity which might cause an increase in the rate of oxygen elimination. Scholander (1940) found a steady and constant oxygen elimination from the blood of a seal during submergence. He also reported no correlation between the amount of struggling and the rate at which the oxygen was eliminated from the blood. Since this seal had previously survived submersion for almost 18 min, I suspect that the oxygen storage potential of the seal was not filled to capacity before the lethal dive. The degree to which the diving bradycardia was maintained suggests that circulatory adjustments, including peripheral vasoconstriction and maintenance of flow to the vital organs (heart, brain) were normal.

Why the seal failed to respond to resuscitation might be explained by events following submersion, including the rise in heart rate to apneic levels. Scholander (1940) said that the greatest disaster in diving comes first in recovery. It is during recovery and resumption of

peripheral perfusion that high concentrations of lactate enter the blood, causing a rapid drop in pH. Perhaps in this case, the combined effects of severe asphyxia and radical pH change could have damaged the respiratory centers and prevented reflex resumption of respiration.

### Brain Weights

Brain weight-body weight ratios of ringed seals are compared with those of other species in Table 8. The larger seals have larger brains, but a much lower brain weight/LBM value.

## DISCUSSION

Morphological studies, blood-oxygen analysis and physiological experimentation on the ringed seal has indicated the existence in this species of diving adaptations comparable with those of other phocid seals. A large oxygen storage capacity is observed in the circulating blood, and the cardiovascular adjustments, as evidenced in ECG records and accompanying morphological adaptations, implies selective use of oxygen stores for perfusion of vital organs during extended submersion.

The oxygen store available to the diving seal is a function of the PCV, oxygen capacity and blood volume. The PCV's of the seals are high compared with those of terrestrial mammals. The ringed seal mean PCV reported here (53.2%) is not significantly different from those reported for harbor, elephant, or Weddell seals (Fig. 12). Geraci and Smith (1975) reported a mean PCV of 63.0% for shot ringed seals and 68.5% for

Table 8. Ratio of brain weight to body weight for four species of phocid seals.

| Species | Age (yr.) | TBM (kg) | LBM (kg) | Brain weight (gm) | Brain weight/LBM (%) |
|---|---|---|---|---|---|
| Ringed seal (#1) *Phoca (Pusa) hispida* | 3 | 23 | 12.0 | 136 | 1.13 |
| Ringed seal (#2) | 1.5 | 15 | 10.0 | 129 | 1.29 |
| *Ringed seal | 2 | 17.3 | 9.4 | 180 | 1.91 |
| *Ringed seal | 2 | 24.1 | 14.3 | 171 | 1.20 |
| *Harbor seal *Phoca vitulina* | (adult) | 50 | 35 | 260 | 0.74 |
| †Weddell seal *Leptonychotes weddelli* | (adult) | 400 | 240 | 500 | 0.21 |
| †Elephant seal *Mirounga angustirostris* | (subadult) | 910 | ‡546 | 900 | ‡0.16 |

* Data obtained from Alaska Department of Fish and Game, Fairbanks, Alaska.

† Data obtained from Professor Robert Elsner, Institute of Marine Science, University of Alaska, Fairbanks, Alaska.

‡ Derived - see Appendix I.

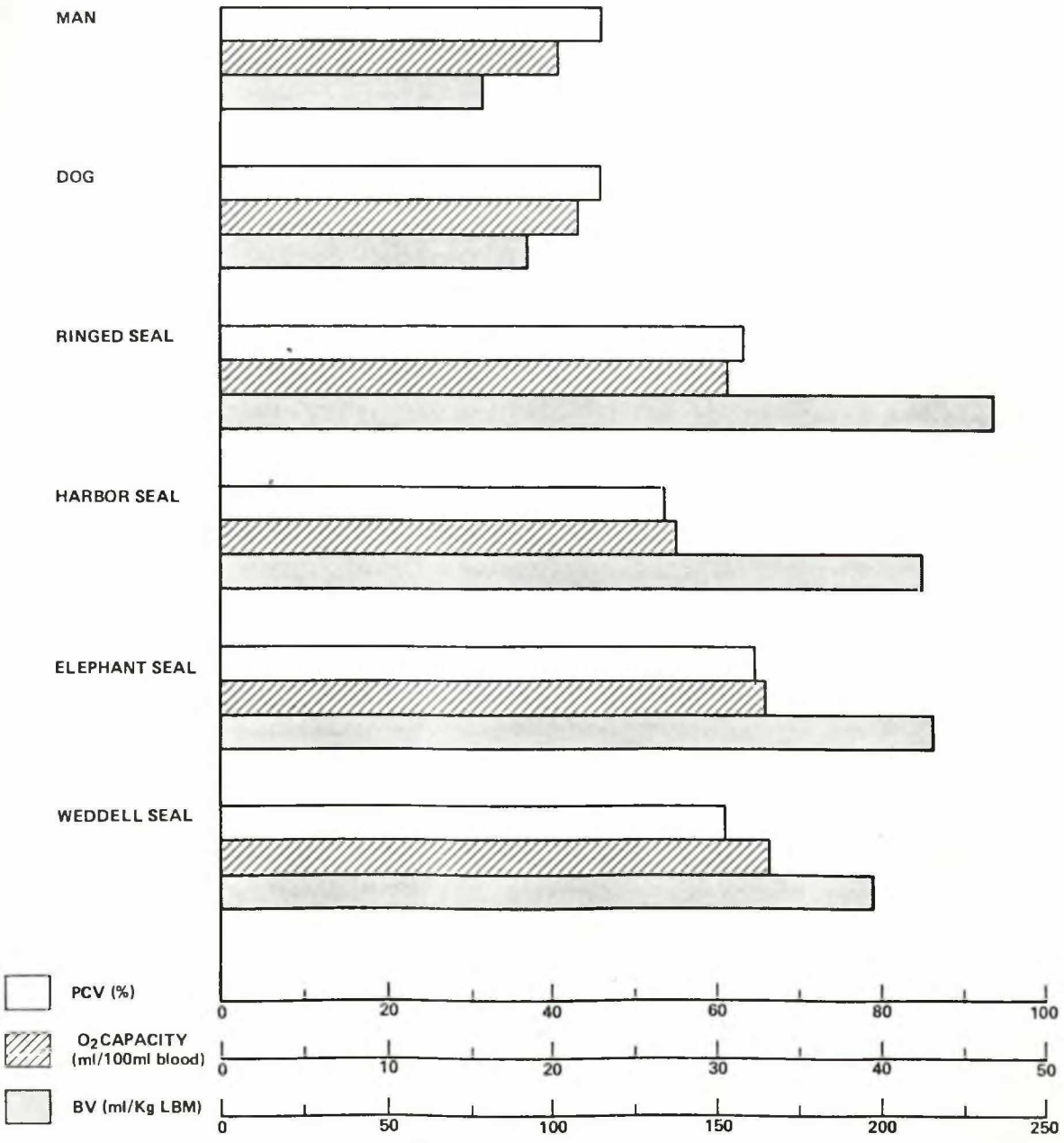


Figure 12. Comparison of mean blood characteristics for man, dog, and four species of phocid seals (data from Tables 1, 2, 3 and 7).

netted wild ringed seals. They considered the values for the shot seals to be normal. The high PCV for the netted seals was believed to be related to stress which results in neurohumoral events leading to contraction of the spleen, forcing additional erythrocytes into the general circulation. The value in the shot seals (63.0%) is higher than the highest value (61.3%) obtained in this study. The lowest value in this study was 42.0%, lower than mean values reported for man and dog. I assume that the difference between the wild ringed seals and the captive seals was the result of differences in their health and nutritional state. The lower values in the experimental seals may reflect poor condition. Certainly, the lowest value was from a seal that obviously was ill. The addition of such low PCV's in the calculation of mean probably resulted in a lower than normal mean for healthy wild animals.

Ringed seal hemoglobin concentration is not significantly different from values reported for Weddell, elephant and harbor seals. However, Geraci and Smith (1975) report mean concentrations of 24.5 g % for shot ringed seals and 26.5 g % for netted seals, both of which are higher than the mean from this study. Because hemoglobin concentration is a function of the packed cell volume, the higher concentrations reported by Geraci and Smith reflect the higher packed cell volumes reported.

The measured oxygen capacity of the experimental ringed seals (mean, 30.74 ± 1.64 ml $O_2$/100 ml whole blood) was similar to those reported for other seals (cf. Table 2). Oxygen capacity is in part a function of PCV and Hb concentration. The mean value for the ringed seals is not significantly lower than the stoichiometric relationship

indicates. Since the mean hemoglobin concentration was 23.7%, the predicted oxygen capacity was 31.76 ml $O_2$/100 ml whole blood or only 1.02 ml more than the measured values.

Blood volume determinations yielded 234 ± 35.5 ml/kg LBM for the experimental ringed seals. This value is higher than the proportional blood volumes reported for harbor and Weddell seals (Table 1), but probably lower than that of the elephant seal, which has a greater BV/TBM. The large standard deviation for the ringed seal's blood volume is due, in part, to the highest value, 314 ml/kg LBM, which may be an error. In this case, following injection of the isotope into the EDIV, I was unable to withdraw blood from the EDIV into the syringe in order to flush out any remaining isotope. This suggested that the placement of the needle in the EDIV had changed prior to the aspiration attempt, in which case, a portion of the isotope may have entered tissues other than the blood. This would result in calculation of a larger dilution volume, i.e., a larger blood volume. Subsequent experiments were conducted by injecting the isotope through a catheter entering the EDIV which negated the possibility of needle displacement and improper injection of isotope.

St. Aubin *et al.* (1978) reported the mean blood volume of the ringed seal as 226 ml/kg LBM, which is comparable to the findings in the study.

The total quantity of oxygen available to supply the metabolic demands of the animal is termed the total oxygen capacity ($TO_2$). Ringed, harbor, and Weddell seals have similar quantities of oxygen available (Table 9) to meet metabolic demand of the lean tissue mass ($TO_2$/kg LBM).

Table 9. Comparison of total oxygen capacity and total oxygen capacity/LBM for four species of phocid seals.

| Species | $O_2$ capacity (ml $O_2$/100 ml blood) | Total blood volume (TBV) (liters) | *Total $O_2$ capacity (liters $O_2$) | LBM (kg) | Total $O_2$ capacity/ kg LBM (liters/kg) |
|---|---|---|---|---|---|
| Ringed seal *Phoca (Pusa) hispida* | 30.74 | 2.67 | 0.82 | 11.4 | 0.072 |
| Harbor seal *Phoca vitulina* | 27.90 | †7.50 | 2.09 | 35.0 | 0.060 |
| Weddell seal *Leptonychotes weddelli* | 31.60 | ‡55.75 | 17.62 | 240.0 | 0.073 |
| §Elephant seal *Mirounga angustirostris* | 32.00 | 196.60 | 62.91 | 546.0 | 0.115 |

* Total $O_2$ capacity = TBV x $O_2$ capacity

† Total blood volume presented for the harbor seal is a calculated TBV for an adult based on the LBM of the adult, using the BV/LBM determined for a subadult harbor seal maintained in this laboratory.

‡ Lenfant *et al.*, 1969.

§ See Appendix I.

The elephant seal appears to have a greater $TO_2$ to lean body mass than the others. Proportionally the harbor seal could store 2.6 times as much oxygen as the ringed seal, the Weddell seal 21.5 times and the elephant seal 76.7 times as much.

Heart rate response in the ringed seals to submersion was similar to that in the other species. An example of a restrained dive episode with a harbor seal, using the same equipment and technique as with the ringed seals, is shown in Figure 13. There was abrupt bradycardia at the beginning of the dive; a low heart rate achieved shortly into the dive was maintained until emersion. This sequence of events is also observed in asphyxiated Weddell seals (Elsner, *et al.* 1970b). Although the elephant seal develops a very slow heart rate during submersion, the bradycardia is less abrupt and intense than in the smaller species (VanCitters, *et al.* 1965).

While the four seal species are similar in blood parameters, their dive durations are not similar (Table 4). Even the unrestrained dives of the Weddell seal are longer than those of the others, and the harbor seal can achieve durations several minutes longer than ringed seals. These differences correspond approximately to differences in body size, which suggest correlation with brain/body weight and total oxygen capacity, rather than with degree of physiological adaptation.

The brain, which is the organ most sensitive to hypoxia, is a significant factor limiting the duration of oxygen stores during a dive. The brain of the ringed seal is smaller than those of harbor, Weddell and elephant seals (Table 8), but its brain mass/LBM is much greater than in

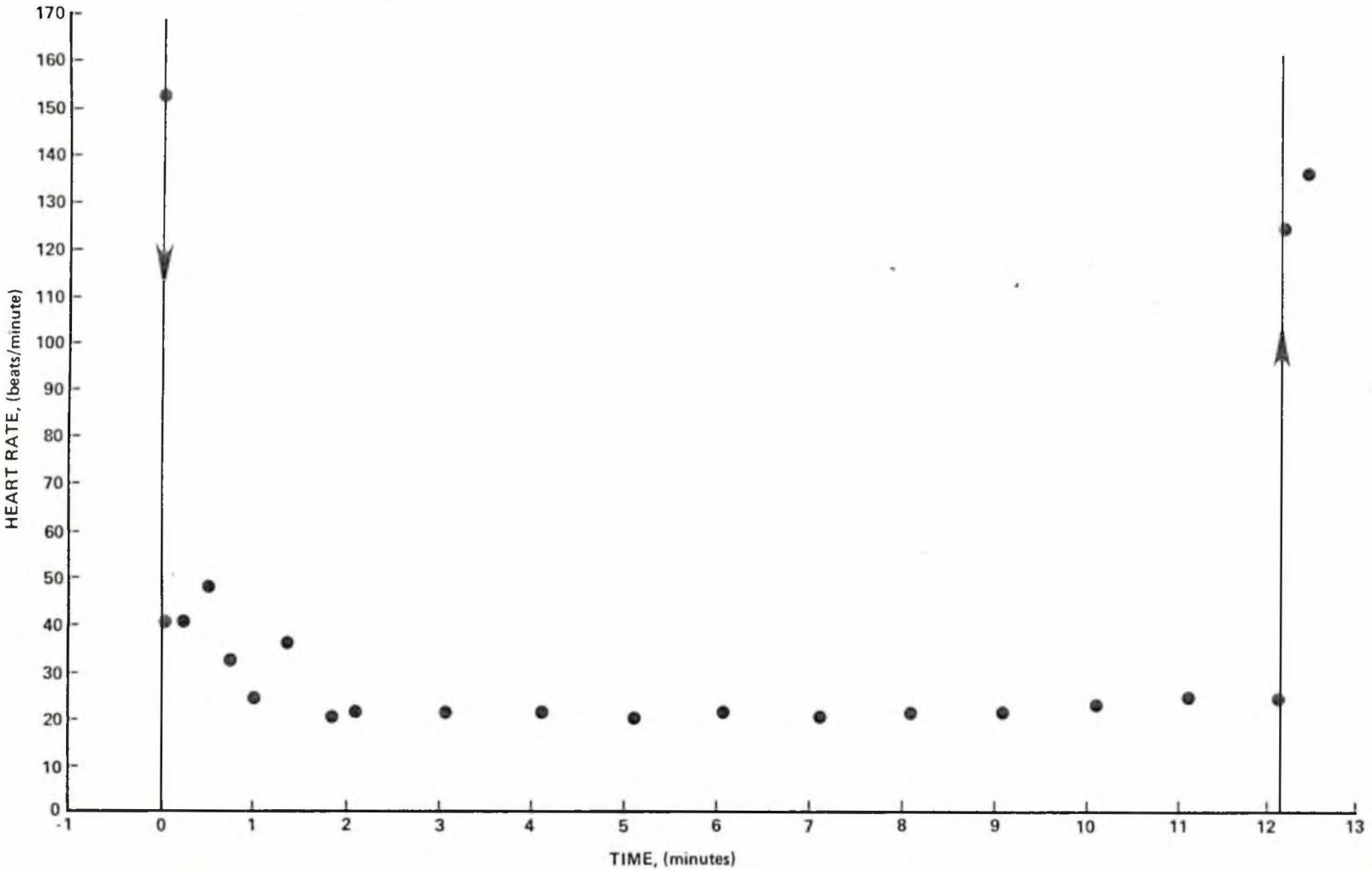


Figure 13. Typical heart rate of a harbor seal during a forced dive.

the other seals. Although the oxygen storage capacity of blood per unit body weight in all of these species is similar, the total $O_2$ capacity available during a dive is not similar, because the total blood volume is proportional to body size. The relatively large brain and small $TO_2$ of the ringed seal in contrast to the relatively small brain and large $TO_2$ of the Weddell seal apparently result in very different durations of dives in these ecologically similar species.

Utilizing the total oxygen capacity values from Table 9 and the brain weights from Table 8, the comparative total $O_2$ capacity/brain weight were:

ringed seal = 0.82ℓ/0.154kg = 5.32 $\ell O_2$/kg brain

harbor seal = 2.09ℓ/0.26kg = 8.05 $\ell O_2$/kg brain

Weddell seal = 17.62ℓ/0.50kg = 35.24 $\ell O_2$/kg brain

elephant seal = 62.91ℓ/0.90kg = 69.89 $\ell O_2$/kg brain

These proportions indicate that the Weddell seal has a $TO_2$ capacity/kg brain mass 6.6 times that of the ringed seal and 4.4 times that of the harbor seal, which would account in part for their differnet dive durations. The elephant seal appears to have twice the $TO_2$/kg brain mass as the Weddell seal but is not known to dive for as long. While there tends to be correlation between $TO_2$/kg brain and dive duration (Fig. 14), the relationship is not sufficiently close to account for all of the difference between species in dive durations. This relationship is described by the regression equation Log $y = 0.38 + 0.02\ x$ ($r = 0.72$).

Records of dive durations show the Weddell seal as capable of diving for up to 60 min which is 2.6 times the dive duration of the ringed

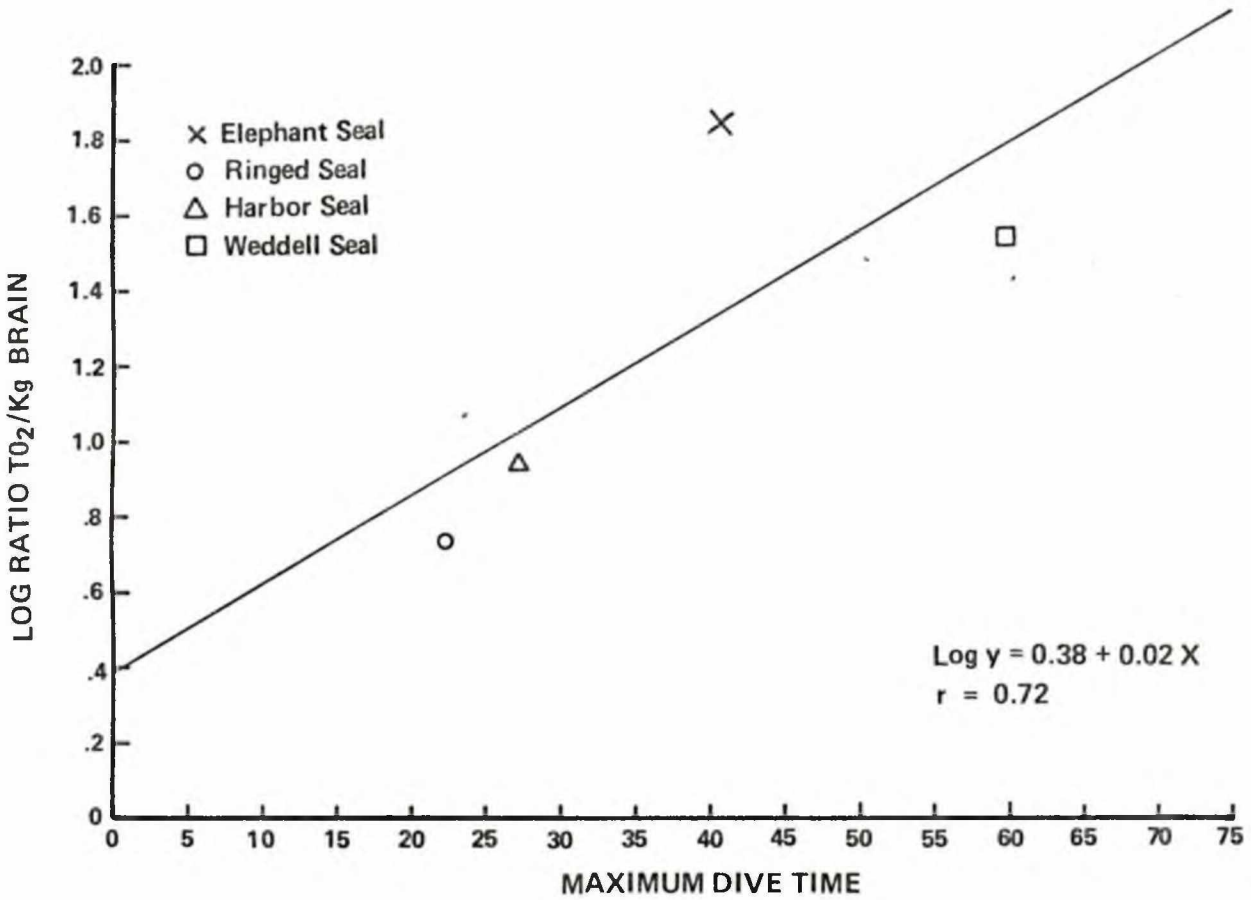


Figure 14. Log ratio of average $TO_2$/kg brain vs. maximum dive time.

seal and 2.1 times that of the harbor seal (Table 4). Taking the Weddell seal as 1, the dive duration ratio for ringed, harbor, elephant and Weddell seals in 0.4:0.5:0.8:1, whereas the $TO_2$/BM ratio is 0.15:0.23:1.98:1. The differences between these ratios suggests that either the ringed and harbor seals are able to utilize the available $O_2$ more efficiently in the dive or that the ratios are not strictly representative. Both the harbor seal and Weddell seal when hypoxic are capable of extracting oxygen from the blood to levels of 10 mmHg $PaO_2$, hence there is no difference in the physiological capability to extract oxygen to low levels of arterial oxygen pressure. Also, considering brain metabolism constant, there cannot be a difference in the efficiency of oxygen utilization by the brain. The only other tissues perfused during the dive are the heart and lungs. The metabolic demand of these tissues must be considered in the final analysis. Their proportion of the LBM must be considered along with the brain mass. This additional tissue mass would affect the vital tissue mass/LBM figures and tend to increase the smaller species $TO_2$/vital tissue mass values more so than for the larger species, resulting in ratios more similiar with the dive ratios.

The speculation that diving durations are limited by the ratios of vital tissue mass/body size (which determine the minimal obligatory oxygen consumption) has been considered by several investigators. Harrison and Tomlinson (1960) noted that the larger and older the seal, the longer it can dive. Since the brain mass of a young animal is larger in proportion to its body and BV than in adults of the same species,

the proportion of $TO_2$/brain mass is less and results in predictably shorter dive duration in young seals. Lenfant *et al.* (1970) also observed that relative to kilograms of active tissue, the Weddell seal has a blood oxygen storage capacity 1.7 times that of the harbor seal, from which they predicted that the diving duration of the Weddell seal should be proportionally greater as well.

The ringed seals used in this study were young animals. Because of the youthfulness of these seals, their ratio of $TO_2$/brain mass probably was lower than in older animals, hence the experimental animals should not have been capable of dive durations as long as those of adult ringed seals. The TBM of adult ringed seals (Smith, 1973) is approximately 2 to 3 times that of the experimental animals utilized in this study. Therefore the diving capabilities indicated by these seals probably were less than those of wild adults and may not be strictly comparable with the data for adults of other species. Parsons (1977), while investigating ringed seal metabolism, observed that one ringed seal dived freely in a laboratory pool for 20.7 min; this seal weighed 32.5 kg, a larger seal and an apparently longer diver than the seals used in this investigation.

Kooyman (1975) predicted the maximum breath-holding capacities of a 450 kg seal and a 50 kg seal, based on percentages of basal metabolic rates required for cerebral and myocardial $O_2$ consumption during submersion. He concluded that blood volume and body $O_2$ stores change in direct linear proportion with body size, but metabolism changes geometrically, so that the smaller animal is at a disadvantage, by a higher oxygen consumption rate and smaller $O_2$ store.

Kooyman's estimate of breath hold capacity of seals based on oxygen stores and aerobic metabolic rate during submergence, if determined for a 910 kg elephant seal indicates a longer dive duration than observed for the Weddell seal. Because the dive duration and $TO_2$/BW value for the elephant seal do not correspond with the suggested trend, there must be other features that have not been considered to explain this discrepency. It is very possible that the elephant seal in indeed an exceptionally long diver, a point yet to be investigated.

Evidence obtained from this investigation indicates that the ringed seal is capable of enduring submergence asphyxia for 30% longer than predicted from $TO_2$/BW (Fig. 14). There is no doubt that such diving capability is beneficial to a seal living in the ocean, particularly in ice covered zones where access to air is limited. That the Weddell seal can dive for 60 min surely facilitates movement beneath Antarctic ice, enabling the seal to swim great distances without surfacing to breath. The comparative diving adaptations of the Weddell seal, harbor seal and ringed seal indicate no significant differences in physiological adaptations, i.e. $O_2$ capacity/kg LBM and dive response, enabling the Weddell seal and ringed seal to occupy ice zones.

## CONCLUSIONS

Physiological adaptations have evolved in phocid seals enabling them to dive for extended periods. The primary adaptive features are high oxygen storage capability, selective use of the oxygen stores, and

tolerance to reduced levels of arterial oxygen pressure. This investigation of ringed seal physiology and diving capability indicates that adaptive features such as high level of oxygen stores and the capability to selectively utilize that oxygen during a dive, also are present in the ringed seal. The principal differences between the compared species are their size and capability to endure prolonged submersion asphyxia. In view of the nearly identical physiological responses and relative oxygen storage capability (liters $O_2$/kg LBM), their differences in duration of dives appears to be a consequence of body size which determines total oxygen stores available to vital tissue mass. More precisely, it is the ratio of the total oxygen stores to the vital tissue mass (primarily the brain) that determines differential capacity for diving duration in these species. This does suggest that size difference, rather than a physiological difference between the Weddell seal and ringed seal may be the most important aspect to consider as an adaptive advantage to the Arctic vs the Antarctic shore-fast ice zones. According to Stirling (1977) it is because of the presence of surface predators in the Arctic, that the ringed seal has a selective advantage in being small, permitting its use of subnivian lairs as protection against predation.

As introduction to this thesis, I speculated that the prolonged diving capability of the Weddell seal was advantageous for existence in the shore-fast ice habitat of Antarctica. This speculation had been put forth previously by various investigators. Undoubtedly a capability for long duration dives enables the Weddell seal to search beneath

the ice for food, for breathing holes and for open leads. I considered the question that since the ringed seal is the ecological counterpart of the Weddell seal, then, does the ringed seal too have the capacity for long dives? Results of physiological analysis and diving experiments indicate the adaptative features and mechanisms known as diving adaptations to be similiar in the ringed seal as in the compared species. The primary observable differences are body size and capability to endure prolonged diving asphyxia.

The correlation between body size ($TO_2$/kg vital tissue mass) and dive time indicates that large phocid seals are capable of diving for longer periods than small phocids. The Weddell seal and ringed seal, although ecological counterparts, have adapted different strategies to contend with the shore-fast ice habitat. Their primary difference is in body size (and resultant diving capability).

Long duration diving is not an adaptation to shore-fast ice *per se* but to the unique characteristics of the Weddell seal. Ice alone seems not to impose ecological restrictions on phocid seals, other than that they must have the capability for maintaining or finding breathing holes where and when necessary.

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APPENDIX I. TBV, $TO_2$, LBM, $TO_2$/kg LBM and BW/LBM are derived values for the elephant seal based on the following data and assumptions.

Data

$O_2$ capacity (Table 2) 31.60 ml $O_2$/100 ml blood (Lenfant *et al.*, 1970)

BV/TBM (Table 1) 148 ml/kg (Simpson *et al.*, 1970)

Adult weight (Table 8) 910 kg (Elsner, personal communication)

(BW) Brain weight (Table 8) 900 gm (Elsner, personal communication)

Assumptions

1. Assume BV/TBM (Table 1) comparable to that of adult seal
2. Assume adult seal to be 40% fat

Derivations

1. TBV = .216 ℓ/kg TBM x 910 kg = 196.6 liters
2. $TO_2$ = .320 ℓ $O_2$/ℓ blood x 196.6 ℓ = 62.9 ℓ $O_2$
3. LBM = 910 kg TBM - (.40 x 910) = 546 kg
4. $TO_2$/kg LBM = 62.9 ℓ $O_2$ ÷ 546 kg = 0.115 ℓ $O_2$/kg
5. BW/LBM (%) = (.9 kg ÷ 546 kg)(100) = 0.16